

A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe

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SYNOPSIS. The form-genus *Neuropteris* was initially established for compound leaves or fronds, whose pinnules had a constricted base and a non-anastomosed venation, and which are mainly found in the Carboniferous. Using a combination of frond/leaf architecture and cuticular features, it is now possible to divide this artificial taxonomic concept into nine more closely circumscribed and homogenous form-genera: *Neuropteris sensu stricto*, *Laveineopteris*, *Macroneuropteris*, *Margaritopteris*, *Neuralethopteris*, *Neurocallipteris*, *Neurodontopteris*, *Paripteris* and *Sphenoneuropteris*. In the palaeobotanical literature of the last half century (since 1940), fifty-seven adequately circumscribed species have been identified from Europe as belonging to *Neuropteris* in its traditional, broad sense (a further forty-four species names have been used, but are either based on inadequate type specimens, or have proved to be later synonyms of other species). Of these fifty-seven 'good' species, fifty-one can be assigned with reasonable confidence to one or other of the nine form-genera mentioned above. That the classification provides a reasonably robust expression of the natural relationships of the species is suggested by the fact that competition appears to have been greater between species of the same form-genus than between species of different form-genera. It is possible to correlate the distribution of some of these form-genera with the palaeoclimatic model that has been proposed based on coal ball evidence. For instance, *Neuropteris sensu stricto* and *Neuralethopteris* appear to have belonged to plants that favoured slightly wetter conditions within Carboniferous equatorial swamps. *Laveineopteris*- and *Paripteris*-bearing plants seem to have been less environmentally constrained, although a change between wetter and drier conditions seems to correlate with a change in the species present. The group as a whole seems to have been most diverse in the peat-accumulating swamps of the Carboniferous equatorial belt, but with clear differences in the

species present in the paralic and intra-montane basins. In the higher southern palaeolatitudes of Gondwana, the group is absent. In the higher northern palaeolatitudes of Angara and Kazakhstan it is also largely absent, with the exception of some possible parippterid species.

INTRODUCTION

The study of Upper Carboniferous palaeobotany in Europe has tended to follow two distinct lines, which may be summarized as coal ball studies and adpression studies. In recent years, the coal ball petrifications have attracted most attention, and have yielded considerable information on the anatomy and thereby the affinities of the plants. The importance of this work is indisputable, but coal ball fossils can only give a partial view of the Late Carboniferous equatorial vegetation. For one thing, they only preserve plants that grew in the peat-accumulating habitats. Although this was the commonest habitat in the swamps, the acidic, water-logged substrate was normally low in oxygen and nutrient, which restricted the variety of plants it could support. Also, coal balls only formed where sea water could percolate through the peat deposits (Scott & Rex 1985). Where the peats formed in a lower delta plain setting (e.g. eastern North America, the Ukraine) there can be a good record of coal balls, but in middle or upper delta plain settings, or intra-montane basins, they are absent. Over much of Europe, coal balls are restricted mainly to just one coal seam in the lower Langsettian, with only a very few other known examples in the Yeomanian, upper Langsettian and topmost Duckmantian (this is excluding the silicified limnic peats in the Stephanian and basal Permian of southern France). For a general review of coal ball distribution, see Phillips (1980).

Of much wider occurrence in the European Upper Carboniferous are plant adpressions. These preserve quite a different part of the equatorial vegetation – mainly that growing on the raised levee banks within the swamps. Although forming a much smaller proportion of the original biomass, taphonomic bias has caused them to dominate the adpression record (Gastaldo *et al.* 1989). Also, because the edaphic conditions were not as extreme, the levees supported a much more diverse vegetation than the peat-accumulating habitats.

The abundance and diversity of the adpression assemblages gives them considerable potential significance for understanding the Late Carboniferous tropical vegetation, but there are a number of widely-perceived drawbacks. The majority of identifiable adpressions are fragments of foliage with (except in some ferns) little direct evidence of reproductive structures. Most 'angiospermocentric' neobotanists give such foliar organs a low taxonomic status, and this attitude has tended to rub off on palaeobotanists ('One good fertile specimen of a given species will tell far more than any quantity of sterile ones' – Andrews 1961). This viewpoint is given support by the traditional generic taxonomy developed by Brongniart (1822) for leaf fossils, and which is still being used in some quarters. It is based on pinnule morphology and venation, and is quite clearly artificial, often hiding natural relationships and differences between species. It ignores the fact that many of these Carboniferous leaves were architecturally complex structures, with many characters of potential phylogenetic value. By viewing them holistically and incorporating such details as leaf architecture into their taxonomy, a

far more robust and natural classification can be developed (e.g. Gothan 1941, Laveine 1967, Zodrow & Cleal 1988, Cleal & Shute 1991a).

Another perceived difficulty with studying Upper Carboniferous adpressions is that they show little anatomical detail. Up to a point, this is a valid criticism, at least when compared with the quality of information that can be determined from coal ball petrifications. However, it should be remembered that in many other parts of the geological column petrifications are absent or rare. It has nevertheless been possible to determine many anatomical details from adpressions, particularly of the epidermis through cuticle studies (e.g. Thomas & Masarati 1982, Kerp 1991). Because of taphonomic factors, such as post-mortem tectonic deformation, cuticles are not as easy to prepare from Carboniferous adpressions as they often are from Mesozoic material. Nevertheless, they can sometimes be obtained from Carboniferous foliage fossils, providing data that can be of considerable taxonomic importance (e.g. Barthel 1961, 1962, Cleal & Zodrow 1989, Cleal & Shute 1991a).

The present paper brings together the results of the authors' studies on one particular group of adpressions which are particularly abundant in the Upper Carboniferous of Europe: fragments of pteridospermous fronds that were traditionally assigned to the form-genus *Neuropteris* Brongniart, and now referred to as neuropteroid fronds. By combining evidence of frond architecture (e.g. Gothan 1941, Laveine 1967, Zodrow & Cleal 1988, Cleal & Shute 1991a) and epidermal structure (Barthel 1961, 1962, 1976, Cleal & Zodrow 1989, Cleal & Shute 1991a, 1992), a revised generic classification of the fossils was introduced by Cleal *et al.* (1990). The first goal of the present study was to test the robustness of this classification. This was done by checking every species that has been recorded from Europe in the last half century, to see what proportion can be assigned to the more natural form-genera in the Cleal *et al.* classification.

As a by-product of doing this check, we have built up a database of the geographical and temporal distribution of species in each of the genera. This has allowed us to see if any patterns can be elucidated, which may have palaeogeographical or palaeoclimatic significance. Such distributional work is not novel in the Carboniferous (see Cleal 1991 for a review). However, by looking at the species distributions in the context of more natural form-genera, it is believed that more meaningful patterns will be revealed.

These fronds mostly belong to the order of plants known as the Trigonocarpaceae (sometimes also referred to as the Medullosales). The order, which is only known from the lowland, palaeoequatorial deposits of the Carboniferous and Lower Permian, consisted mainly of shrubs and small trees, although one small liana-like species has recently been described by Hamer & Rothwell (1988). They characteristically had large dissected leaves or fronds, sometimes up to 7 metres long (Laveine 1986), but more typically 1–2 metres long (e.g. Cleal & Shute 1991a). In addition to the form-genera covered by the present study, other trigonocarpacean fronds include *Odontopteris* (Brongniart) Sternberg, 1825,

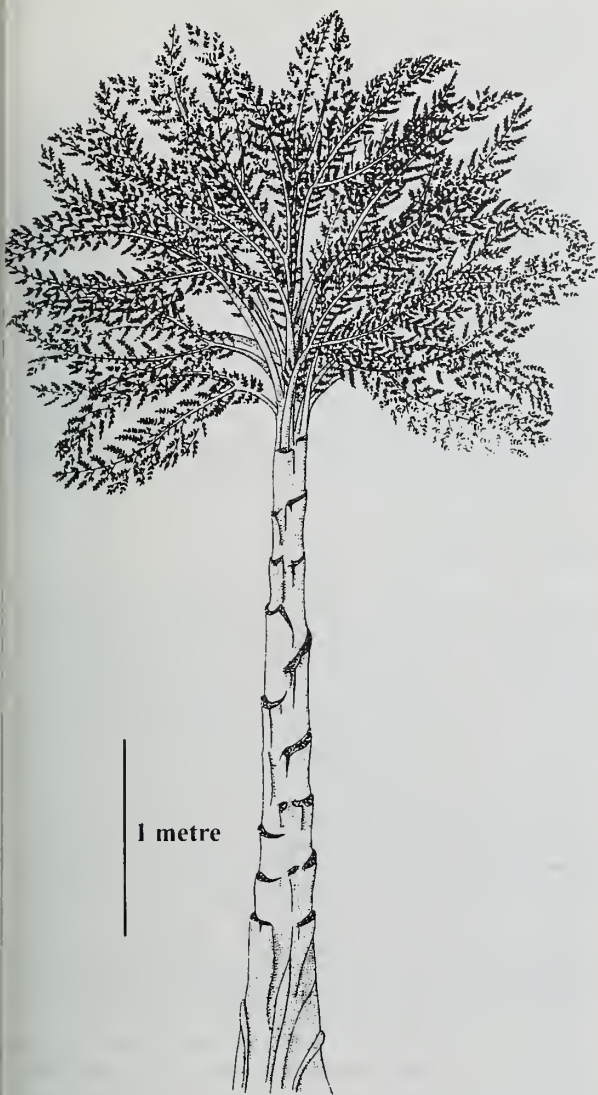


Fig. 1 Reconstruction of *Neuropteris heterophylla*, drawn by Mrs. Pauline Dean (prepared for part of the Evolution of Wales Gallery, National Museum of Wales, Cardiff, See Thomas & Cleal 1993:19).

von Bernhardt, 1800 (see Cleal & Shute 1991b), *Callipteridium* (Weiss) Zeiller, 1888a, *Alethopteris* Sternberg, 1825, *Lonchopteris* Brongniart, 1828, *Linopteris* Presl, 1838, and *Reticulopteris* Gothan, 1941. Traditionally, it has been assumed that both the ovuliferous and microsporangiate fructifications were attached directly to the vegetative fronds, and a number of examples showing this have been described in the literature (e.g. Dix 1932, Darrah 1937, Zodrow & McCandlish 1980). However, there has recently come to light evidence that in some of the trigonocarpaleans they formed more or less complex strobilus-like structures, attached either in an axillary position to the frond, or directly to the cauline axis (Drinnan *et al.* 1990, Laveine *et al.* 1991). The individual ovules were often large, robust structures, up to 8 cm long (Gastaldo & Matten 1978), which probably relied on flotation for dispersal. The microsporangia clusters, on the other hand, were mainly small delicate structures, containing either

monolete or (in the Potonieaceae) trilete prepollen (Millay & Taylor 1979).

The group is not just important as a numerically significant component of the Trigonocarpaceae (at least as represented in the fossil record). Many species in the neuropteroid complex have proved stratigraphically useful. Preeminent is *Neuropteris ovata*, the base of whose range is the main index to the base of the Westphalian D stage, but many others also play an important role; in the biostratigraphical classification of Carboniferous strata outlined by Cleal (1991), 2 zones and 6 subzones are named after neuropteroid species. It is thus important to the biostratigrapher as well as the evolutionary palaeobotanist to place the taxonomy of these fronds on a firm footing.

METHODS

This analysis has been based on data extracted from palaeobotanical literature published over the last half century. A starting date of 1940 was chosen as providing both a realistic volume of literature to search, as well as an almost complete cover of geographical areas yielding plant fossils in Europe. In certain areas where there has been extensive work on Carboniferous palaeobotany, only the most recent monographs have been used, although where necessary they have been supplemented by other works which may document any species omitted from the monographs. Full details of this can be found below in the section 'Sources of data'.

Every neuropteroid species that has been identified from the Carboniferous and Permian of Europe during this half century has been assessed. It has then been either:

1. Assigned to one or other of the frond form-genera outlined below in the section 'Generic classification' and, where necessary, a new combination proposed; or
2. Assigned to the group of species that cannot be classified in one or other of the frond form-genera; or
3. Assigned to an earlier published species as a synonym, with brief reasons given, or a reference given to another authority, for the proposal; or
4. Assigned to the list of *nomen dubia* species, that were originally described on inadequate material.

The resulting taxonomic section of this paper thus includes for each species that is accepted as valid (1) its name, (2) a synonymy list (see further comments below), (3) reasons for generic assignment, (4) any other comments, and (5) its geographical and stratigraphical distribution.

Synonymy lists

The lists given are not complete and only include those references that are significant for defining the species: the basionym, the combination accepted in this analysis, where the type specimen(s) are published if they are not included in the protologue, and where there is a photographic record of the type specimen(s) if the original reproduction was an engraving or similar illustration. It also includes those species that have been published since 1940, which are now thought to be later synonyms.

In order to clarify the lists, they have been annotated using a system comparable to that outlined by Matthews (1973).

However, it has been found useful to add to the range of signs originally given by Matthews, and the full set as used here is listed below.

- * The protologue of the basionym.
- § The valid publication of the combination accepted here.
- T The type specimen(s) when not published in the protologue, or photographic illustrations of them if the original illustrations were poor.
- ? The inclusion of this reference is provisional due, for instance, to poor illustration.
- The present authors accept responsibility for including this in the synonymy; if a species is included as a synonym without the '.', then it is based on another authority, which is quoted at the end of the reference.
- v The authors have seen the specimens in question.

Statistical analyses

The database built up as a result of this review has been subject to statistical analysis, to try to determine distributional patterns. Univariate and bivariate statistics were calculated using the Arcus Pro-II package (version 2). The statistics are straightforward and require little explanation other than that the method of least-squares was used in the regressions.

Cluster analyses were performed using the MVSP package, on an IBM PC-AT computer. This package is particularly useful, as it provides a routine (SORTDATA) for showing which species cause the clusters to form. Jaccard's Coefficient was used for the measure of similarity between assemblages, as this gives no weight to cases where a particular species is absent from both samples (Sokal & Sneath 1963). This was deemed preferable to measures such as the Simple Matching Coefficient, which takes such double-absences of a species into account, and which might distort the results with localities which have been only incompletely sampled. Clustering was performed using the unweighted pair group strategy, which on the whole tends to give a better resolution of the clusters in binary data than the mathematically simpler single linkage strategy (Sokal & Sneath 1963). A detailed discussion of the relative merits of the various similarity measures and clustering strategies available can be found in Sokal & Sneath (1963) and Everitt (1980).

It is widely recommended (e.g. Sneath & Sokal 1973) that similarity measures of this type should be investigated using both cluster and ordination methods. To this end, the matrices of Jaccard's Coefficients were submitted to Gower's Principal Coordinates Analysis (PCO), again using the MVSP package, which provides a series of two-dimensional graphical plots. The results generally confirmed the patterns observed using the cluster analysis, but did not have the merit of such a concise graphical presentation. As they add nothing to our conclusions, the results of these PCO analyses have not therefore been included in the paper.

The cluster analyses were performed on matrices of binary (presence/absence) data for the various areas. Our information was not really amenable to establishing quantified values for the abundance of the species in the different areas. In any case, it has recently been shown that such presence/absence data in fact produce better results than quantified data in establishing patterns of geographical distributions of plant fossils, even where the quantified data can be reliably measured (Boulter *et al.* 1993).

GEOLOGICAL BACKGROUND

Chronostratigraphical terminology

This paper is not intended as a biostratigraphical analysis. The stratigraphical data is included only as a general guide and is limited to the distribution between stages. For brevity, the stage names have been abbreviated using a similar scheme to that used by Harland *et al.* (1982). Unfortunately, however, Harland *et al.* only used the European stages for the Viséan and Namurian; for the higher part of the Carboniferous and the Permian, they switched to the Russian classification. We are therefore proposing a list of abbreviations for the full set of European stages, as summarized in Fig. 2. This figure also gives an estimate of the duration of each of the stages, based on the radiometric data summarized by Leeder (1988), and which includes the dates derived from sanidine crystals from tonsteins.

Sources of data

The following provides a summary of the areas into which the geographical distributional data have been divided, with a statement as to the sources from where the palaeobotanical information has been extracted. The locations of these areas are plotted in Fig. 3 on a palaeogeographical map for the Upper Carboniferous, using the same numbering of the areas as given below. The chronostratigraphical range of strata that yield plant fossils in each of the areas is shown using the abbreviations mentioned above. Some areas where strata of an appropriate age are known to occur will not be found below. These include the Campine Basin of Belgium, the Flöha Basin of southern Germany, the North Sudetic Basin of the Czech Republic, the Reșița and Svinița basins in Romania, and the various basins in the Balkans. They have been excluded from this analysis because the literature on the plant fossils is inadequate and/or more than 50 years old.

1. *South-West UK (Arn-Can)*. The British records have been divided between those south and north of the Wales-Brabant Barrier. Those from the south belong mainly to what Calver (1969) called the South-West Basin, and refers to the South Wales, Forest of Dean and Bristol-Somerset coalfields (it excludes the Kent Coalfield, which is part of the Franco-Belgian Basin). The records of neuropteroid species is based mainly on the illustrations in Crookall (1959), although his taxonomy has needed considerable modification (partly done by Laveine 1967). Some additions have also been made following the biostratigraphical analysis of the Welsh fossils by Cleal (1978).

2. *Pennines (Asb-WeD)*. This is taken in a wider sense than originally envisaged by Calver (1969), and includes both his Pennines and Scottish basins. Records of plant fossils from Scotland are relatively few but those that there are seem to differ little from those of the Pennines. The main source of data on the neuropteroid species in this area is Crookall (1959).

3. *Franco-Belgian Basin (Pnd-WeD)*. This includes the Nord-Pas-de-Calais Coalfield in northern France, and the Mons-Charleroi-Namur Coalfield in Belgium (it also includes the Kent Coalfield in Britain, but there are few illustrated records of plant fossils from there). Neuropteroid species

Subsystems	Old Stages	Old Sub-Stages	New Stages	Stage Abbreviations	Duration of Stage in million years
Lower Permian	Autunian		Autunian	Aut	2(?)
Upper Carboniferous	Stephanian	Stephanian C	Stephanian C	StC	1
		Stephanian B	Stephanian B	StB	2
		Stephanian A	Barruelian	Bar	2
			Cantabrian	Can	1
	Westphalian	Westphalian D	Westphalian D	WeD	2
		Westphalian C	Bolsovia	Bol	3
		Westphalian B	Duckmantian	Duc	2
		Westphalian A	Langsettian	Lan	2
	Namurian	Namurian C	Yeadonian	Yea	1(?)
		Namurian B	Marsdenian	Mrd	2
			Kinderscoutian	Kin	2
		Namurian A	Alportian	Alp	1
			Chokierian	Cho	2
			Arnsbergian	Arn	2
			Pendleian	Pnd	2
			Brigantian	Bri	4(?)
Lower Carboniferous	Viséan		Asbian	Asb	5(?)

Fig. 2 Stratigraphical schemes for the strata known to yield neuropteroid fossils. It includes the Heerlen set of stages and substages, the set of stages currently accepted by the IUGS Subcommittee on Carboniferous Stratigraphy, and a newly-revised set of abbreviations for the stages. Also given is the estimated duration of each stage, based mainly on Leeder (1988).

have been documented better in these coalfields than probably anywhere else in the world. This is mainly due to the monographs by Stockmans (1933) and, perhaps more significantly, by Laveine (1967). Additional data have also been taken from Stockmans & Williére (1953, 1955), van Amerom & Lambrecht (1979) and Paproth *et al.* (1983).

1. *S. Limburg (Lan-Bol)*. This lies between the NW Germany basin and the Kempe Basin of Belgium. There have been few studies on the palaeobotany of this basin in recent years, the only ones with illustrations of neuropteroid axa being by Jongmans (1953a, 1953b, 1954). In order to attempt a more comprehensive assessment of the fossils from here, data has also been incorporated from Jongmans & Gøthan (1915).

2. *NW Germany (Arn-WeD)*. This area is based mainly around the Ruhr Coalfield, but also includes the smaller coalfields in the Osnabrück Highlands (Ibbenbüren, Piesberg and Hügell), which appear to belong to the same basin (Josten *et al.* 1984). The most recent monograph on the neuropteroid axa from here is by Gøthan (1953) and most of the records quoted herein are based on this analysis. Additional records have been taken from Josten (1983, 1991) and Josten & Laveine (1984).

3. *NE Germany (Kin-Bol)*. This is part of the paralic basin that has been discovered in deep boreholes in the region of Rostock, on the northern coast of what used to be the German Democratic Republic. Plant fossils from the Namurian have been documented by Kahlert (1979). The

first illustrated records of plant fossils from the Westphalian were by Daber (1963a, 1967), but the stratigraphical information provided is not sufficiently detailed for the purposes of this study. More detailed evidence has recently been provided by Gründel (1992) and Kahlert (1992), and have been used as the basis of the records incorporated in this study. The claims that the upper part of this sequence extends up into the Westphalian D or even Stephanian (e.g. Kahlert 1992) are based on doubtful evidence such as the presence of conifer remains and is not accepted here.

7. *Lublin (Asb-Bol)*. This represents the easternmost extension of the belt of paralic deposits that extended across northern Europe; the highest marine strata known here can be correlated with what is known as the Vanderbeckei Marine Band in Britain, and marks the boundary between the Langsettian and Duckmantian stages. The best documentation of neuropteroid foliage from here is by Migier (1966), but there are also useful but unillustrated summaries provided by Migier (1980) and Kotasowa & Migier in Bojkowski & Porzycki (1983).

8. *Zwickau-Oelsnitz (WeD)*. This was an intra-montane basin formed in a small depression in present-day Saxony, SE Germany (Pietzsch 1962). The neuropteroid taxa from here have been documented by Daber (1955, 1957).

9. *Saxony (Aut)*. This refers to the Erzgebirge (or Ore Mountains), Döhlener, Weißig and North Saxony Volcanic basins, which lie between the Saale Trough and the Central Bohemian Basin. They contain upper Stephanian and Rot-

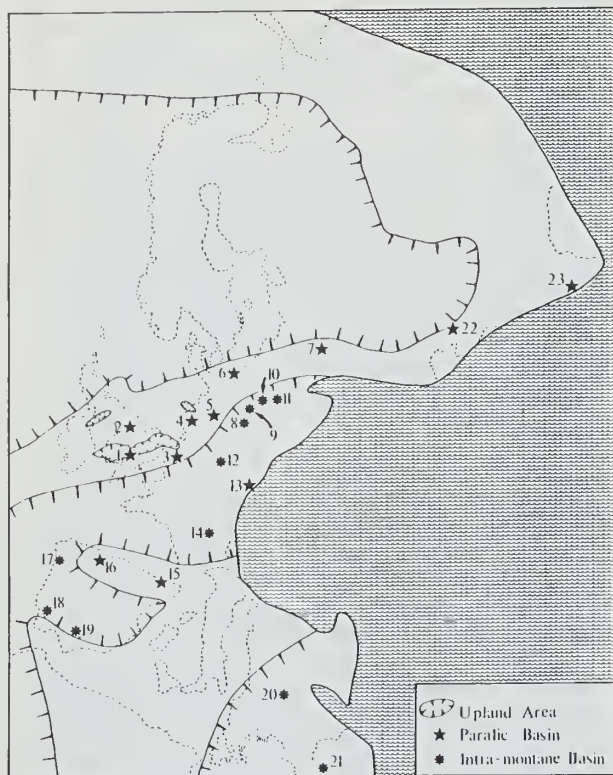


Fig. 3 Palaeogeographical map of Europe in the Late Carboniferous, showing location of areas that have yielded neuropteroid adpressions. Map based mainly on the Stephanian reconstruction of Scotese (1986), with modifications adapted from Bless *et al.* (1977) and Haszeldine (1984). The marine areas, both shelf and deep ocean, are shaded. Locality numbers: 1 – South-West United Kingdom; 2 – Pennines; 3 – Franco-Belgian Basin; 4 – S. Limburg; 5 – NW Germany; 6 – NE Germany; 7 – Lublin; 8 – Zwickau-Oelsnitz; 9 – Saxony; 10 – Upper Silesia; 11 – Intra-Sudetic Basin; 12 – Saar-Lorraine; 13 – Alps; 14 – Massif Central; 15 – Pyrenees; 16 – NW Spain; 17 – N. Portugal; 18 – S. Portugal; 19 – S. Spain; 20 – Svoge; 21 – Turkey; 22 – Donets; 23 – N. Caucasus.

liegende strata, although only the latter have yielded plant fossils. The degree to which the basins were originally connected is still not clear, but Barthel (1976) has shown that, from a floristic standpoint, they combined to form a more or less homogeneous unit. Barthel provides a brief account of the geology, together with a detailed documentation of the plant fossils.

10. Upper Silesia (Asb–WeD). This basin straddles the Polish-Czech border. The name comes from the Upper Silesia Coalfield in Poland (Bojkowski & Porzycki 1983), while in the Czech Republic it is represented by the Ostrava-Karvina Coalfield (Dopita & Havlena 1977). Up until the early Namurian, it was part of the paralic belt that stretched across northern Europe. Thereafter, however, marine influence ceased, and it became an intra-montane basin. The neuropteroid taxa from the Namurian and lower Westphalian of this basin are documented by Stopa (1957), Kotasowa (1968) and Purkyňová (1971). The upper Westphalian plant

fossils are less well documented, although some useful data is provided by Kotasowa (1979).

11. Intra-Sudetic Basin (?Asb–Aut). This also straddles the Polish-Czech border. Traditionally, it was taken to include the Lower Silesia, Podkrkonoší and Poorlická pánev coalfields. However, sedimentological work summarized by Holub *et al.* (1977) suggests that it was part of a larger area of sedimentation, also including the large Central Bohemian 'basin', as well as smaller areas of outcrop such as the Boskovice and Blanice furrows (see also comments by Havlena 1953 and Wagner 1977). It is in this wider sense that we use the term Intra-Sudetic Basin. Most of the neuropteroid taxa are documented by Němejc (1949) and Havlena (1953).

12. Saar-Lorraine (Duc–WeD, Bar–Aut). This was an intra-montane basin, lying between the Rheno-Hercynian and Saxo-Thuringian zones, and now straddling the Franco-German border. The deep borehole Saar-1 has proved that deposition started in the late Viséan (Weingart 1976). However, the exposed part of the sequence, and that which has yielded virtually all known neuropteroid taxa, ranges from upper Duckmantian to Autunian, with a stratigraphical gap from the top Westphalian D to upper Baruelian. The neuropteroid taxa from here have been documented by Cleal (1985) and Laveine (1989), with additional contributions by de Jong (1974), Doubinger & Germer (1975a, 1975b), Boersma (1978) and Cleal & Zedrow (1989). Also, although it was published before the starting point that we have selected for this study, the exceptionally illustrated monograph by Bertrand (1930) cannot be ignored (although his species have not been included in the synonymy).

13. Alps (?Cho–Aut). Caught up in the complex tectonic deformation of the Alps are numerous patches of Carboniferous strata yielding plant fossils. The heavy tectonism means that the fossils are on the whole fragmentary and yield no cuticle. Also, the dislocation of the strata means that it is often difficult to place them in any sort of coherent stratigraphical continuum. Nevertheless, enough material has been collected over the years to allow many neuropteroid species to be recognized from the Austrian (Fritz *et al.* 1990), Swiss (Jongmans 1960) and French (Greber 1965) alps. Most material comes from the less tectonized Internal Zone (also known as the Briançonnais Zone in France), although some material has also come from the External Zone.

14. Massif Central (Can–Aut). Within this upland area in France lie a series of mainly small, intra-montane basins that developed during the Stephanian as a result of Variscan tectonic activity. The most important include St. Étienne (the eponymous area for the Stephanian Series), Autun (the eponymous area for the Autunian Stage), Commeny, Brive, Blanzay, Bert, Decize and Decazeville: a more complete list is provided by Doubinger & Vetter (1985). The definitive work on the plant fossils of this area is Doubinger (1956), who reviewed and partially documented the upper Stephanian and basal Permian palaeobotany of all of the major basins. The main drawback of this work is that she persisted in using a number of species described originally by Zeiller (1888a, 1906), despite the fact that the types are totally inadequate and Doubinger herself had no new material. As a consequence, some of these Zeiller species, which otherwise would not have been included, have had to be referred to in this analysis. Other major monographs on the palaeobotany of

individual basins are by Vetter (1968 – Decazeville) and Langiaux (1984 – Blanz).

15. *Pyrenees (Kin, Aut)*. Like the Alps, this area has been subjected to considerable tectonic deformation. Terrestrial Upper Carboniferous and Lower Permian strata occur in a number of small, isolated basins, and plant fossils are widely distributed. However, there are few illustrated records of them in recent years, the only significant exceptions being by Delvolvé & Laveine (1985 – Kin) and Broutin & Gisbert (1985 – Aut).

16. *NW Spain (Mrd–Aut)*. This is an area of Upper Palaeozoic deposits that ranges over parts of Asturias, Palencia and León, and is sometimes referred to as the Cantabrian Zone. It was subjected to major disruption by Variscan tectonics, resulting in sequences containing several angular unconformities, and preserved in a series of disjointed outcrops. Mainly through the work of Wagner and his collaborators, the complex geology has been at least partly unravelled. Wagner (1970) and Wagner & Winkler Prins (1985) provide valuable summaries, and more detailed information can be found in Truyols in Martínez Díaz (1983). As part of this work, extensive collections of plant fossils have been made. Up to the late Westphalian D, deposition was mainly marine, with only intermittent fluvio-deltaic incursions, but at higher levels non-marine strata become increasingly predominant. Consequently, the Marsdenian to Bolsovian plant fossil record is patchy, but from the Westphalian D upwards it is effectively continuous into the Permian. General reviews of the plant fossils are provided by Wagner (1959, 1962, 1966) and Stockmans & Willière (1965), but none are complete. They have therefore been supplemented by the records from individual coalfields: Central Asturia (Jongmans 1952a, Wagner 1971, Wagner & Alvarez-Vázquez, 1991), San Emiliano (Moore *et al.* 1971), Cervera de Pisuerga (Wagner 1960, Cleal 1981), Tejerina (Wagner *et al.* 1969), Guardo (Wagner *et al.* 1983), Ciñera-Matallana (Wagner 1963, 1964), and Sabero (Knight 1983). Also, an undocumented list of Stephanian C fossils by Wagner & Laveine in Wagner & Martínez García (1982) has been included, being the only recent record from strata of this age.

17. *N. Portugal (WeD, StC–Aut)*. Most of the Upper Carboniferous and basal Permian in Portugal occurs in the north of the country, near Oporto (Sousa & Wagner 1983). They represent isolated intra-montane basins in the Central Iberian tectonic zone, and according to Wagner (1983a) can be related to the Carboniferous deposits in S. Spain (see below). Of those containing Westphalian strata, only that at Ervedosa has yielded abundant plant fossils, including neuropteroid fronds. The other basins rich in plant fossils (the Douro and Buçaco basins) are Stephanian C to Autunian in age. The palaeobotany of these deposits is reviewed by Wagner & Sousa (1983).

18. *S. Portugal (WeD)*. This refers to three small outliers that are the only development of continental Upper Carboniferous rocks in southern Portugal. They are the remains of an elongate basin (the Santa Susana Basin) that developed along the fracture-zone that separates the Ossa-Morena and South Portuguese tectonic zones. Much of the sequence is conglomeratic, but there are also coals with finer-grained clastic deposits that have yielded plant fossils. The latter are reviewed by Wagner & Sousa (1983).

19. *S. Spain (Lan, StC–Aut)*. Carboniferous and Permian terrestrial deposits in the southern half of the country are very patchy, being mainly restricted to small, fault-bounded basins. Westphalian plant fossils have been recorded from just two areas: the Villaneuva del Río y Minas Coalfield in Sevilla (Lan – Wagner *et al.* 1983), and Peñarroya-Bélmuez-Espinez (or Guadiato) Coalfield in Córdoba (Wagner 1983a, 1983b, 1990). A third area of Westphalian strata occurs in the Sierra de San Pedro in Cáceres (Wagner 1983a), but there appear to be no records of plant fossils from here.

From higher strata, the best documented assemblages of plant fossils occur near Guadalcanal in northern Sevilla (Broutin 1986) and the Puertollano Coalfield in Ciudad Real (Wagner 1985). In addition, there are records from Henarejos in Cuenca (Wagner *et al.* 1985). Plant fossils have been reported in a number of other outcrops of Autunian strata (reviewed by Wagner & Martínez García 1982, and Martínez Díaz 1983), but none have yielded neuropteroid foliage.

20. *Svoge (?Pnd–?Cho; Yea–Bol)*. This is the most important coalfield in Bulgaria, and represents the remains of an intra-montane basin (Tenčov 1971). The most comprehensive analysis of the Carboniferous plant fossils from here is by Tenčov (1977). Another major coalfield, known as the Dobroudja Basin, has been discovered in eastern Bulgaria below Mesozoic cover (Tenčov & Koulaksuzov 1972) but to date the plant fossils have not been monographed. The palaeobotany of the small upper Stephanian and Permian basins in northwest Bulgaria (Tenčov 1971, 1973) have also not been revised taxonomically in recent years.

21. *Turkey (Yea–WeD)*. Upper Carboniferous occurs in a number of small outcrops near the northern coast of Turkey, the most important being near Zonguldak, Amasra, Pelitova and Azdavay. The stratigraphy is summarized by Kerey *et al.* (1986), who also provide a well documented record of the plant fossils. A more extensive listing of fossils is provided by Jongmans (1955), but is unillustrated and so cannot be judged.

22. *Donets (Bri–Aut)*. The Donets Basin lies on the southern edge of the Russian Platform, and has produced the most important coalfield in eastern Europe. Brief accounts of the Upper Palaeozoic geology of the area are given by Kler *et al.* (1975) and Aizenverg *et al.* (1975). Prior to the very late Viséan, it was exclusively an area of marine-carbonate deposition. From the Brigantian, however, deltaic complexes frequently extended into the basin, and the rest of the Carboniferous consists of alternating marine and non-marine deposits. This has given the basin considerable potential importance for correlating the so-called Heerlen chronostratigraphical classification, that was based on the non-marine sequences of western Europe, and the standardized Russian chronostratigraphy, based mainly on the marine sequences of the Moscow Basin (Wagner *et al.* 1979). The most detailed illustrated documentation of the plant fossils from here have been by Novik (1952, 1954, 1968), although additional unillustrated data are given by Fissunenkov & Laveine (1984).

23. *North Caucasus (?Kin–WeD, StB–StC)*. A number of areas of Carboniferous outcrop occur on the northern slopes of the Caucasus (Kavkaza) Mountains in Georgia. Their geology is outlined by Pogrebnov (1975) and Kler *et al.* (1975). Mainly Tournaisian marine deposits are overlain unconformably by exclusively non-marine Upper Carboniferous

ous deposits. They are of interest as the easternmost Carboniferous plant-bearing deposits of Laurasia, although their assemblages are regarded as having close affinities with those of western Europe, closer in fact than with the geographically nearer Donets. The plant fossils from here are described by Novik (1952, 1978), Shchegolev (1979) and Anisimova (1979).

TAXONOMIC BACKGROUND

Criteria for accepting a species

Most of the species listed in the *nomen dubia* section of this paper are validly published according to the International Code of Botanical Nomenclature, but in our view have been described from insufficient material to demonstrate the range of morphological variation. A knowledge of this variation is essential if a species is to be usable for specimens other than the types, and thus for it to be a viable taxonomic entity (Cleal 1986).

There are no fixed rules for determining if a species has been adequately defined; common sense has to be the main guide. If it is based mainly on isolated pinnules and short fragments of pinna, then 'tens' of specimens are almost certainly needed to demonstrate the variation. If, on the other hand, the specimens represent large segments of primary pinna branches, then the variation may be demonstrable with less than ten. Rarely, if ever, is a single isolated specimen a sufficient basis for describing a new species, no matter how different it may seem to be from existing species.

The generic model

The generic classification used here has been developed from taxonomic schemes proposed by Gothan (1941), Laveine (1967) and Cleal *et al.* (1990). Those of Gothan and Laveine were based on features of gross morphology, primarily of frond architecture, while Cleal *et al.* also used epidermal evidence. In this study, we have also used three other, less well-known form-genera (*Neurodontopteris*, *Sphenoneuropteris*, *Margaritopteris*) to accommodate a small number of species, which would otherwise be unassignable. The main diagnostic characters for each form-genus is summarized in Table 1. In the following section, the systematics of each form-genus is briefly summarized. It should be emphasized that an attempt has been made to make these form-genera as far as possible natural clusters of species, and are thus form-genera in the sense of Cleal (1986) and Visscher *et al.* (1986), rather than in the artificial sense given in the International Code of Botanical Nomenclature.

Form-genus **LAVEINEOPTERIS** Cleal, Shute & Zodrow (1990: 489)

TYPE. *L. loshii* (Brongniart) Cleal, Shute & Zodrow

COMMENTS. This was established for the neuropteroid species that have been shown to have large, orbicular cyclopterid pinnules in the lower part of the frond (Figs 4, 5). Such cyclopterids have often been taken to characterize all of the imparipinnate neuropteroid species. As pointed out by Cleal & Shute (1991a), however, cyclopterids are only known



Fig. 4 *Laveineopteris loshii* (Brongniart) Cleal *et al.* Copy of von Roehl (1868: fig. 17), showing orbicular cyclopterids attached near the dichotomy of the primary rachis. Origin: Hibernia Colliery, near Gelsenkirchen, the Ruhr, Germany. Here reproduced at $\times 0.28$ of original specimen.

attached to a very small range of species, all of which also show a distinctive set of cuticular characters, such as the virtual absence of intercellular flanges on the abaxial pinnule surface, the absence of multicellular trichomes, and the weak differentiation of the costal and intercostal fields of the adaxial pinnule epidermis (Fig. 17C,D).

It is important to emphasise that the laveineopterid cyclopterids are different from the swollen pinnules present at the base of the true neuropterid fronds. As pointed out by Cleal & Zodrow (1989), these cyclopterid pinnules have a markedly different epidermal structure from the 'ordinary' pinnules in the main part of the frond. Also, they were not originally orientated in the same plane as the rest of the frond. Their function is still unclear, but it is unlikely to have been simply photosynthetic.

The presence of cyclopterid pinnules suggests that *Laveineopteris* is more closely related to the callipteridiums than the neuropterids, since similar cyclopterids are known attached to both *Callipteridium* and *Margaritopteris* (Laveine *et al.* 1977). Unfortunately, little is known of the epidermal structure of the callipteridiums to support this view.

The anatomy of the rachides is of a type usually associated

Table 1 The gross morphological and cuticular characters used to diagnose the form-genera covered in this paper. Expanded from Cleal & Shute (1992: Table 1).

	<i>Laveineopteris</i>	<i>Neuropteris</i>	<i>Macroneuropteris</i>	<i>Neurocallipteris</i>	<i>Neuradelethopteris</i>	<i>Parapteris</i>	<i>Neurodontopteris</i>
Stomata on only abaxial surface (-) or both surfaces (+)	-	-	-	±	-	-	+
Costal and intercostal cells on adaxial surface different (+) or similar (-) from one another	-	+	-	+	+	-	+
Abaxial cuticle with strong (+) or virtually no (-) anticlinal walls	-	+	+	+	+	-	+
Stomata anomocytic (An), brachyparacytic (Br), cyclocytic (Cy) or amphicyclocytic (Am)	An	An/Br	Br/Cy	Cy/Am	Br(?)	An(?)	Cy
Papillae on abaxial surface	-	+	+	+	+	-	+
Multicellular trichomes on abaxial surface	-	+	+	-	-	-	+
Orbicular or reniform cyclopterid pinnules in lower part of frond	+	-	-	-	-	-	-
Primary pinna branches bipinnate (2), tripinnate (3) or quadripinnate (4)	3/4	3/4	2/3	3	3	?	2
Pinnules that are normally partially fused to rachis except near base of frond	-	+	-	+	-	-	+
Midvein usually decurrent and extending for <2/3 pinnule length (+) or non-decurrent and extending for >2/3 pinnule length (-)	-	+	-	+	-	-	+

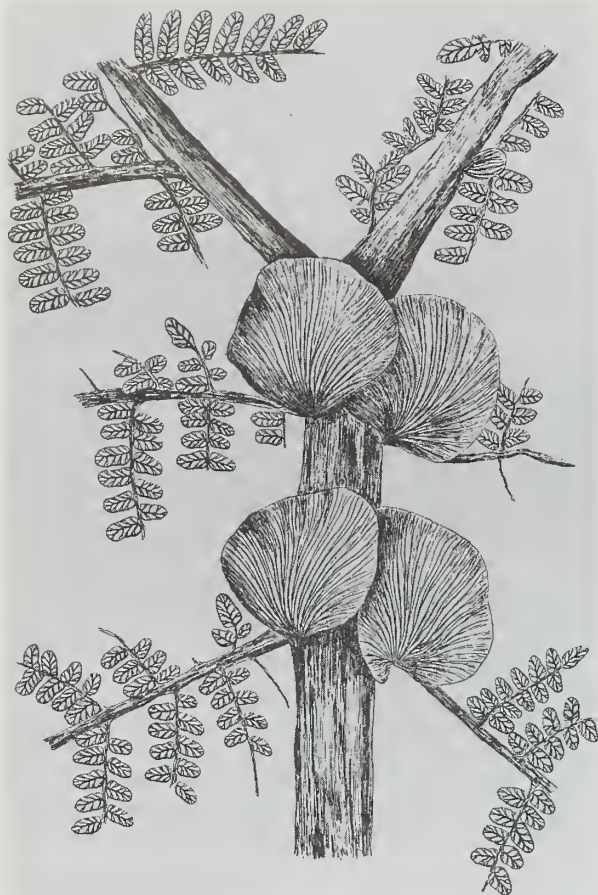


Fig. 5 *Laveineopteris rarinervis* (Bunbury) Cleal *et al.* Copy of Carpentier (1930: fig. 1), showing orbicular cyclopterids attached near the dichotomy of the primary rachis. Here reproduced at $\times 0.7$ life size.

with the Trigonocarpales (Oestry-Stidd 1979). Little is known of the fructifications, other than that large ovules were attached directly to the frond, probably at the end of ultimate pinnae (Kidston 1904).

Form-genus **MACRONEUROPTERIS** Cleal, Shute & Zodrow (1990: 488)

TYPE. *M. macrophylla* (Brongniart) Cleal, Shute & Zodrow

COMMENTS. Most neuropteroid fronds have a dichotomy of the primary rachis producing tripinnate or occasionally quadripinnate branches. In some species, however, the dichotomy of the primary rachis produces less-divided, essentially bipinnate, primary rachis branches (Figs 6–7). These species also have a number of distinctive epidermal characteristics, such as brachyparacytic or cyclocytic stomata (Fig. 17E,F). It was for this distinctive group of species that Cleal *et al.* (1991) proposed the form-genus *Macroneuropteris*.

The fronds of *Macroneuropteris* are very similar to *Neuropteris sensu stricto*, except that they are less divided. Of particular significance is the presence in at least one macro-neuropterid species (*M. scheuchzeri*) of so-called 'Odontopt-

eris lindleyana'-type pinnules (e.g. Crookall 1959: pl. 57, fig. 1), which can be compared with lacinate pinnules in the lower part of true neuropterid fronds (e.g. Stockmans 1933: pl. 11 fig. 1; pl. 12 fig. 2; Zodrow & Cleal 1988: pl. 4 fig. 3). There is no evidence of the orbicular cyclopterid pinnules of *Laveineopteris* or *Margaritopteris*.

Nothing is known of the fructifications. Beeler (1983) claimed that the rachis anatomy is of a type typical of the Trigonocarpales. However, this was based purely on evidence of association; she could find no such rachides with macro-neuropterid pinnules directly attached.

Form-genus **MARGARITOPTERIS** Gothan (1913: 168)

TYPE. *M. coemansii* (Andrä) Gothan

COMMENTS. Most species included in this form-genus have broadly attached and/or lobed pinnules, and prior to Gothan's protologue were assigned to *Odontopteris* (Brongniart) Sternberg, 1825 or *Sphenopteris* (Brongniart) Sternberg, 1825 (see Laveine *et al.* 1977). However, one species, originally included in *Neuropteris* also belongs here ('*N.*' *multivenosa* Purkyňová). Laveine *et al.* (1977) have shown that it is almost certainly the ancestral form of *Callipteridium*. Nothing is known of the fructifications or stem/rachis anatomy.

Form-genus **NEURALETHOPTERIS** Cremer ex Laveine (1967: 97)

TYPE. *N. schlehanii* (Stur) Laveine

COMMENTS. This form-genus is used for alethopterid-like fronds, in which the pinnules have a constricted base (Fig. 8). Most of its component species were originally described as neuropterids, but they in fact have little to do with that form-genus in its currently defined sense.

The taxonomy of the form-genus has been thoroughly discussed by Laveine (1967), and need not be repeated. Our only disagreement with his analysis concerns the authorship of the taxon. Laveine quotes Cremer (1893), but this is a thesis that was not effectively published. Wagner (1963, 1965) suggested that the name should be resurrected, but provided neither a diagnosis nor type. The first validly published diagnosis is in fact in Laveine's study, who must therefore be taken as the author of the genus.

The architecture of the frond has been established with reasonable certainty by Laveine *et al.* (1992). As with most of the trigonocarpaleans, the frond had a dichotomy of the primary rachis producing two tripinnate primary rachis branches. Most significantly, there appear to be no intercalated elements on the primary rachis branches between the secondary pinnae. The lack of this feature separates *Neuralethopteris* from most of the other neuropteroid fronds and helps confirm that its affinities lies closest with the alethopterids.

There have been a number of reports of sporangial organs attached or closely associated with neuralethopterid fronds (Dix 1932, 1933; Arnold 1949; Jongmans 1954; Stockmans & Willière 1961; Laveine 1967). Dix and Arnold both referred them to the form-genus *Aulacotheca*, but Jongmans identified them as *Whittleseyia*. By studying a range of specimens from a single locality, Stockmans & Willière concluded that this apparent taxonomic difference in fact reflected infraspecific

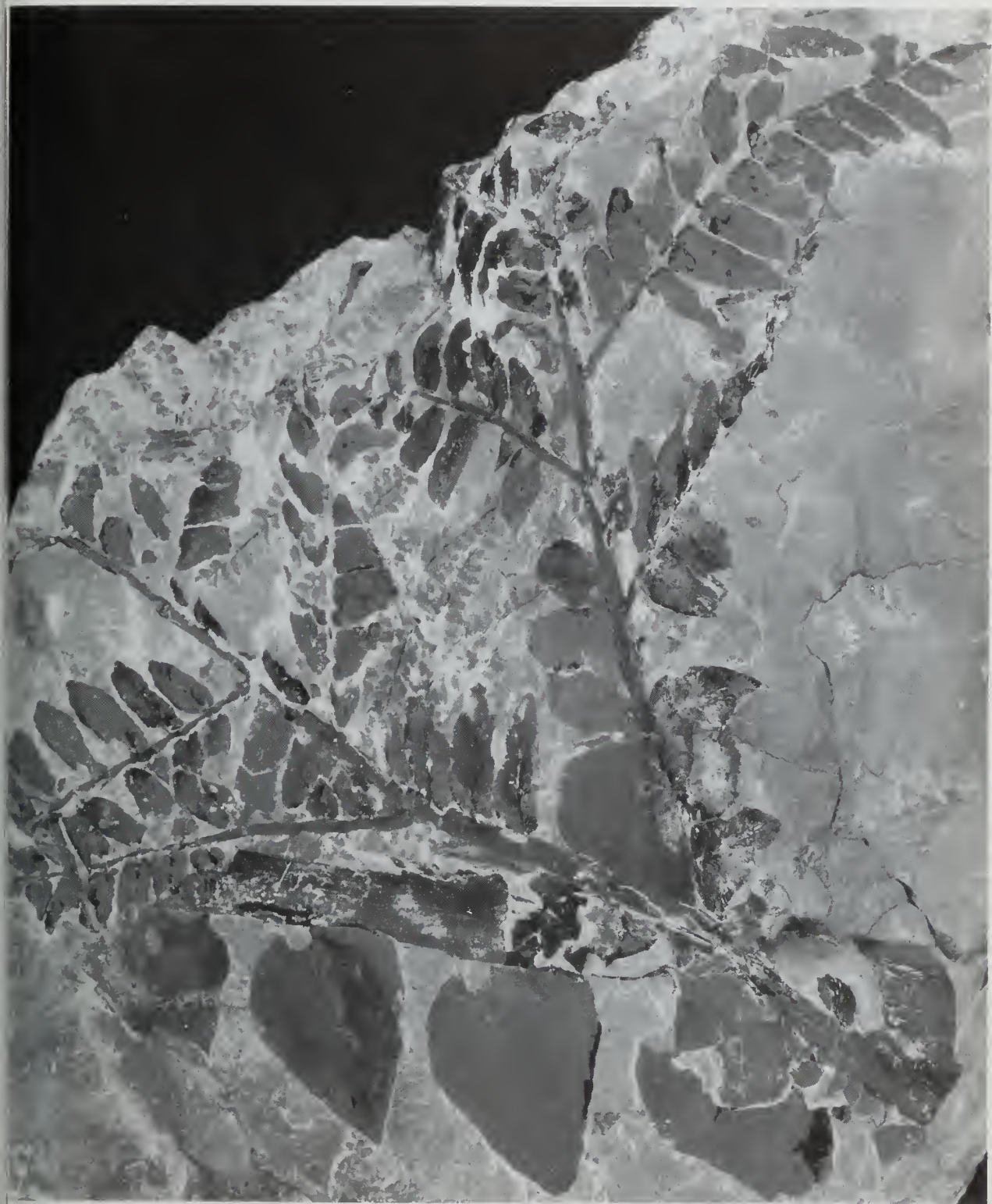


Fig. 6 *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.* Specimen showing lower part of frond. V.2970. Westphalian D, Radstock, Somerset, UK. Natural size.

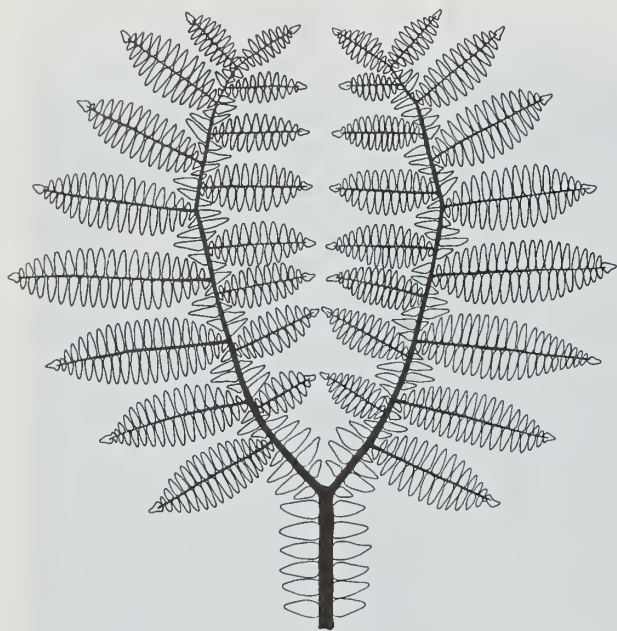


Fig. 7 Reconstruction of *Macroneuropteris* frond (*M. macrophylla* (Brongniart) Cleal *et al.*). Based on work done with Professor J.-P. Laveine.

morphological variation. They therefore proposed the form-genus *Givesia* for the neurolethopterid sporangial organs.

No ovules have been found attached to *Neurolethopteris* fronds, although Jongmans (1954) reported large, *Rhabdocarpus* ovules in close association. There is no available evidence of the stem or rachis anatomy.

Form-genus *NEUROCALLIPTERIS* Sterzel (1895: 283)

TYPE. *N. gleichenioides* (Stur) Sterzel (*Neuropteris gleichenioides* Stur).

COMMENTS. The systematic basis of this form-genus is given by Cleal *et al.* (1990). In essence, it refers to a group of Stephanian and Lower Permian neuropteroid fronds (Fig. 9), which have been shown to have more complex stomatal apparatuses than typical neuropterids (Fig. 10). Relatively little is known of the frond architecture but what information is available (e.g. Šetlík 1980) suggests that it is very similar to that of *Neuropteris sensu stricto*. However, as none of the species are that well known, the genus may not be fully homogeneous. Evidence of fructifications or stem/rachis anatomy is unknown.

In the upper Barruelian to Autunian is found a species which looks very like *Neurocallipteris*, but has an anastomosed venation. This was generally referred to as *Reticulopteris germarii* (Giebel) Gothan, but it is now assigned to a different form-genus, namely *Barthelopteris* Zodrow & Cleal (1993). Thus, just as *Reticulopteris* is the mesh-veined form of *Neuropteris*, and *Linopteris* is the mesh-veined form of *Paripteris*, *Barthelopteris* is the mesh-veined counterpart of *Neurocallipteris*.

Form-genus *NEURODONTOPTERIS* Potonié (1893: 124)

TYPE. *N. auriculata* (Brongniart) Potonié

COMMENTS. This form-genus was originally established for species showing pinnule characteristics intermediate between *Neuropteris* and *Odontopteris*. In this sense, it is clearly an artificial concept. However, there has been a recent reconstruction of the frond (Langiaux 1984: 105) from which a more 'natural' concept for the form-genus can be developed. Obvious characteristics include the smaller and less-divided frond compared with *Neuropteris* (Fig. 12) and the tendency of the pinnules to be fused to the rachis along the basiscopic side. Cuticular evidence also clearly characterizes the type species (described by Barthel 1976, under the incorrect name *Neuropteris cordata* – Z. Šimůnek, pers. comm. 1992). Distinctive features include the pinnules being amphistomatic and the cyclocytic stomata without marked papillae (Fig. 11). The form-genus is in clear need of revision and is used here only to include the type species. The frond architecture suggests affinities with the Trigonocarpaceae. However, there is no evidence of fructifications or stem/rachis anatomy to support this view.

Form-genus *NEUROPTERIS* (Brongniart) Sternberg (1825: xi)

BASIONYM. *Filicites* sect. *Neuropteris* Brongniart (1822: 233)

TYPE. *Neuropteris heterophylla* (Brongniart) Sternberg

COMMENTS. This name was originally established by Brongniart for all fossil frond fragments bearing pinnules with a constricted base and non-anastomosed venation. Subsequent work demonstrated that several clusters of species could be recognized in the traditional concept of *Neuropteris* (Gothan 1941, Laveine 1967, Cleal & Zodrow 1989) but it was not certain which of them included the type species (*N. heterophylla*) and thus was true *Neuropteris*. The problem was solved by the study of the cuticles and frond architecture of the type species by Cleal & Shute (1991a), and allowed the formal re-classification of the group by Cleal *et al.* (1990) (NB. the title of the Cleal & Shute 1991a paper was changed at the last minute and is different to that quoted in the bibliography at the end of Cleal *et al.* 1990). It is the emended concept of *Neuropteris* proposed by Cleal *et al.* (1990) that is used in this paper.

Despite previous preconceptions, *Neuropteris sensu stricto* has pinnules that are often partly fused to the rachis, and have a relatively weakly developed midvein (Fig. 13). Like *Laveineopteris*, the main dichotomy of the primary rachis produces tri- or rarely quadripinnate branches (Figs 14–16). Unlike *Laveineopteris*, however, there are no orbicular cyclopterids attached to the proximal part of the frond. Instead, the primary rachis below the dichotomy bears rachides with enlarged and/or lacinate pinnules attached. Both from their orientation relative to the rest of the frond, and their epidermal structures, these basal pinnules would seem to have simply been photosynthetic structures, not differing significantly in function from the pinnules higher in the frond.

During the middle Westphalian, *Neuropteris* developed progressively more flexuous veins, culminating in the Bolsovian in a fully anastomosed venation (Josten 1962, Zodrow & Cleal 1993). This anastomosed form of neuropterid is



fig. 8 *Neuralethopteris schlehanii* (Stur) Laveine. V.1301. Langsettian (Westphalian A), Oldbury, West Midlands, UK. A, whole specimen, $\times 1$. B,C, close-ups of pinnules, $\times 3$.

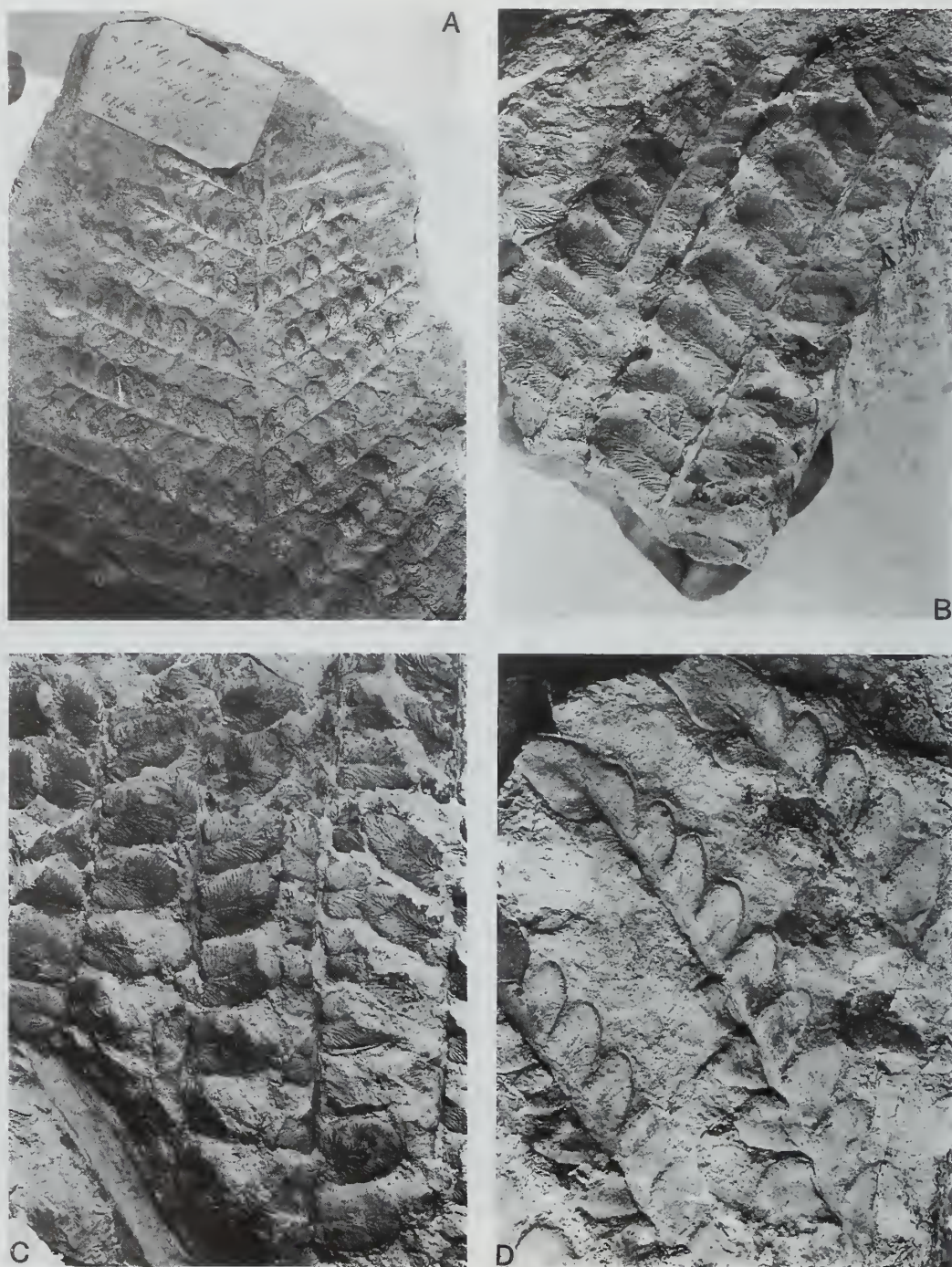


Fig. 9 *Neurocallipteris neuropteroides* (Göppert) Cleal *et al.* Richter Collection, Zwickau Museum, Germany. Lower Porphyrtuff, Planitzer Schichten (Lower Permian), Reinsdorf, Erzgebirge, Germany (type locality). A, $\times 1$. B–D, $\times 1.5$. Illustrations prepared from negatives provided by Professor. M. Barthel.

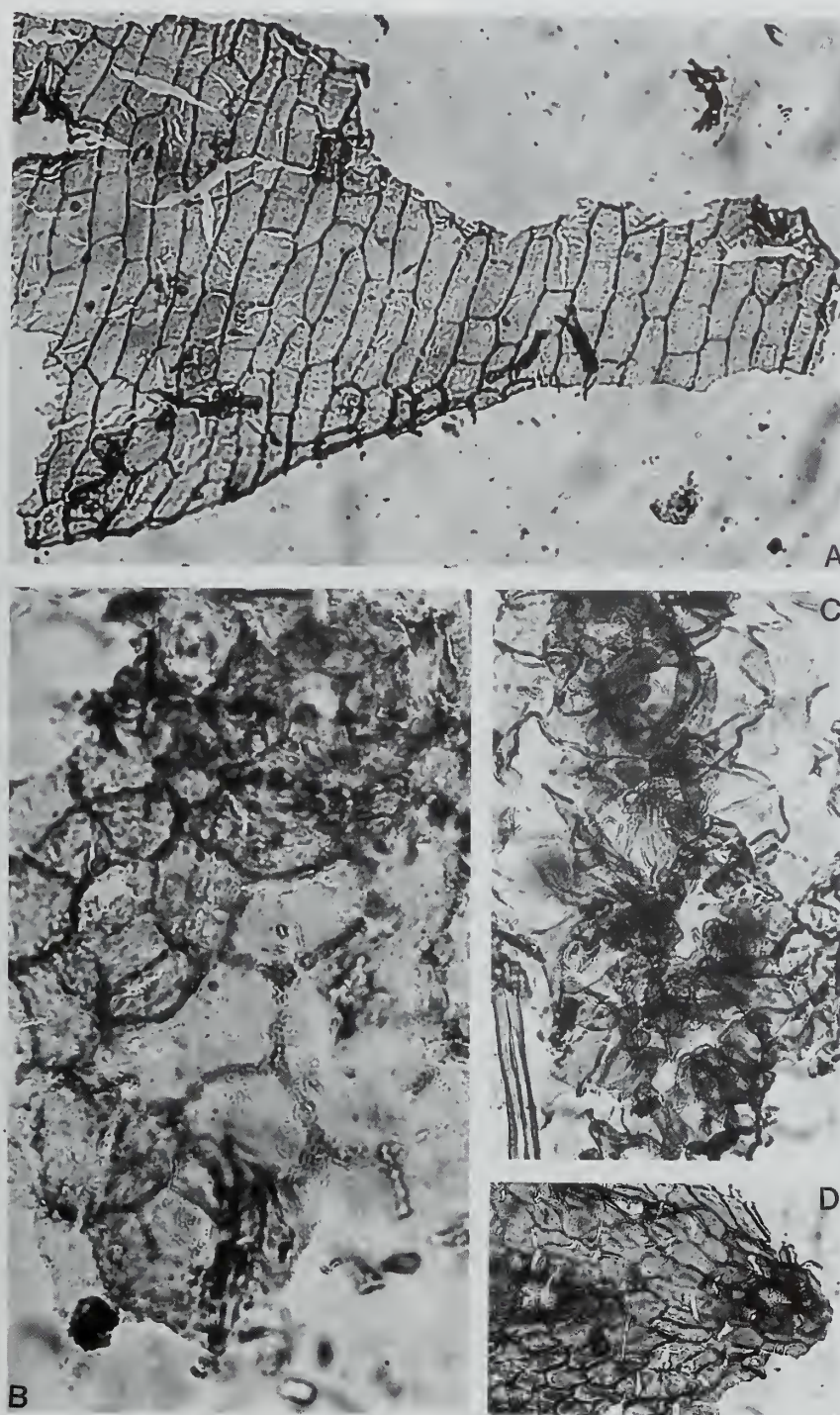


fig. 10 *Neurocallipteris neuropteroides* (Göppert) Cleal *et al.* Slides stored in the Museum für Naturkunde, Berlin. Härtensdorfer Schichten (Lower Permian), Hedwig Shaft (Wilde Collieries), Oelsnitz, Erzgebirge, Germany. A, adaxial cuticle, Slide No. I/89, $\times 200$. B, brachyparacytic stomata on abaxial cuticle, Slide No I/89, $\times 500$. C, papillae surrounding stomata on abaxial cuticle, Slide No II/61, $\times 500$. D, stomata from near the edge of an abaxial cuticle, Slide No. I/89, $\times 200$. Illustrations prepared from negatives provided by Professor. M. Barthel.

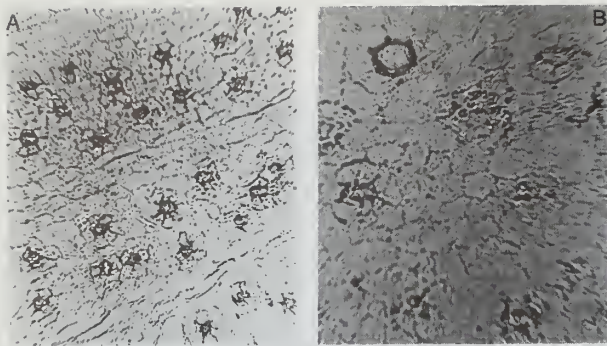


Fig. 11 *Neurodopteris auriculata* (Brongniart) Potonié. Czech Geological Survey, Slide No. 226/1. Lower Stephanian B, Jívka Member, Odolov Formation, Kateřina Mine, Radvanice, Bohemia (Intra-Sudetic Basin). A, bands of stomata in intercostal areas, $\times 50$. B, close-up of cyclocytic stomata, $\times 140$. Photographs provided by Dr Z. Šimůnek.

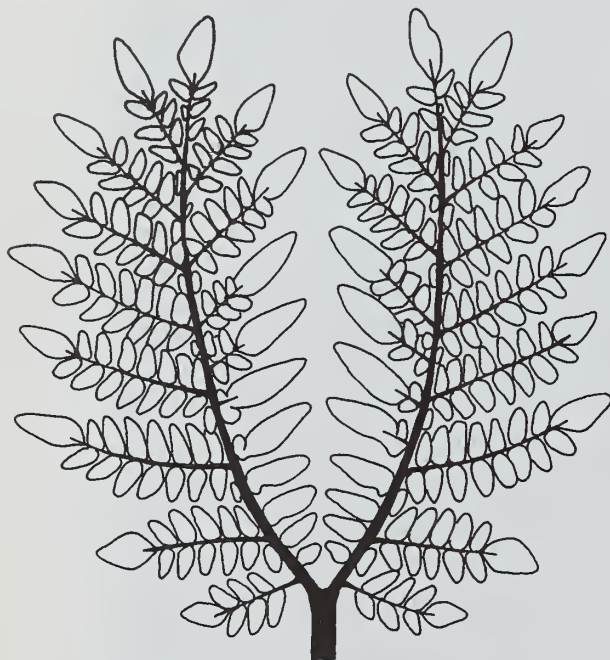


Fig. 12 Reconstruction of *Neurodopteris* frond. Based on Langiaux (1984: fig. 233).

assigned to the form-genus *Reticulopteris* Gothan. In the lower Westphalian D, *Reticulopteris* declines in abundance, then becomes extinct to be replaced by another group of neuropterids centred on the species *N. ovata* Hoffmann. The palaeoecological background to this variation in venation is discussed in the Diversity Analysis section, later in this paper.

Distinctive characters of the pinnule cuticles are the abundant trichomes, especially on the abaxial surface, the well developed intercellular flanges on the abaxial cuticles, and the anomocytic or brachyparacytic stomata (Fig. 17A,B).

Beeler (1983) has demonstrated that *Neuropteris sensu stricto* fronds were attached to stems belonging to the form-genus *Medullosa*, providing strong support for their trigonocarpalean affinities. Evidence as to the fructifications is less

conclusive. Kidston & Jongmans (1911) have reported a sporangial organ attached to a fragment of *Neuropteris* frond, while Darrah (1937) and Zedrow & McCandlish (1980) have reported ovules in apparent attachment. However, no anatomical information has been obtained from these fructifications. Perhaps the most interesting point is that the ovules seem to be attached laterally to a pinna, replacing a lateral pinna, whereas the lavenopterid ovules seem to have been attached to the distal end of the pinna, replacing an apical pinna.

Form-genus *PARIPTERIS* Gothan (1941: 427)

TYPE. *P. gigantea* (Sternberg) Gothan

COMMENTS. The systematic basis of this form-genus has been thoroughly analysed by Laveine (1967). Its distinctive paripinnate frond architecture (paired apical pinnules, intercalated pinnules on the penultimate rachides) separates it from all of the other neuropteroid form-genera (Fig. 16).

There is a mesh-veined counterpart of *Paripteris*, known as *Linopteris* Presl. It would seem that it is the foliage of a distinctive group of trigonocarpalean pteridosperms, which may be referred to as the Potonieaceae (see Cleal, 1993). In addition to the distinctive frond architecture, at least one member of the family (*Linopteris obliqua* Bunbury) has been shown to have stems with a vascular system that is not as dissected as in the other trigonocarpaleans, and when preserved as a petrification is known as *Sutcliffia* (Stidd *et al.* 1975). The ovules are generally assumed to be of the type known as *Hexagonocarpus* (or *Hexapterospermum* when preserved anatomically), and are characterized by a six-fold axial symmetry (Taylor 1966), in contrast to the three-fold symmetry of other trigonocarpalean ovules. Perhaps most distinctive are the male fructifications, which consist of numerous sporangial clusters (individually known as *Potoniea*) formed into a large cone-like structure (Laveine *et al.* 1991). They contain trilete prepollen, in contrast to the monolet prepollen of the other trigonocarpaleans (Stidd 1978).

The morphological evidence for the distinctiveness of the Potonieaceae is also supported by its distribution (Laveine *et al.* 1989). The Potonieaceae originated in the Viséan of China and did not appear in Laurasia until the Namurian. The rest of the Trigonocarpaceae, in contrast, seem to have originated in Laurasia and only a few species are found in China. Most authors still retain the Potonieaceae in the Trigonocarpaceae, but there is increasing evidence that it represents a totally distinct group of pteridosperms, the few similarities (e.g. detailed ovule structure) being a matter of analogy.

Form-genus *SPHENONEUROPTERIS* Shchegolev (1979: 158)

TYPE. *S. elegans* Shchegolev

COMMENTS. This refers to a group of mainly Stephanian fronds that stand apart from most other neuropteroids, in having large, relatively lax pinnules with a low vein density. Wagner (1963) and Knight (1983) put forward evidence to show that at least some of the species ('*N.* *dimorpha*', '*N.* *praedentata*', '*Mixoneura wagneri*') cluster together to form a more natural group, although they did not propose a new name for the group.

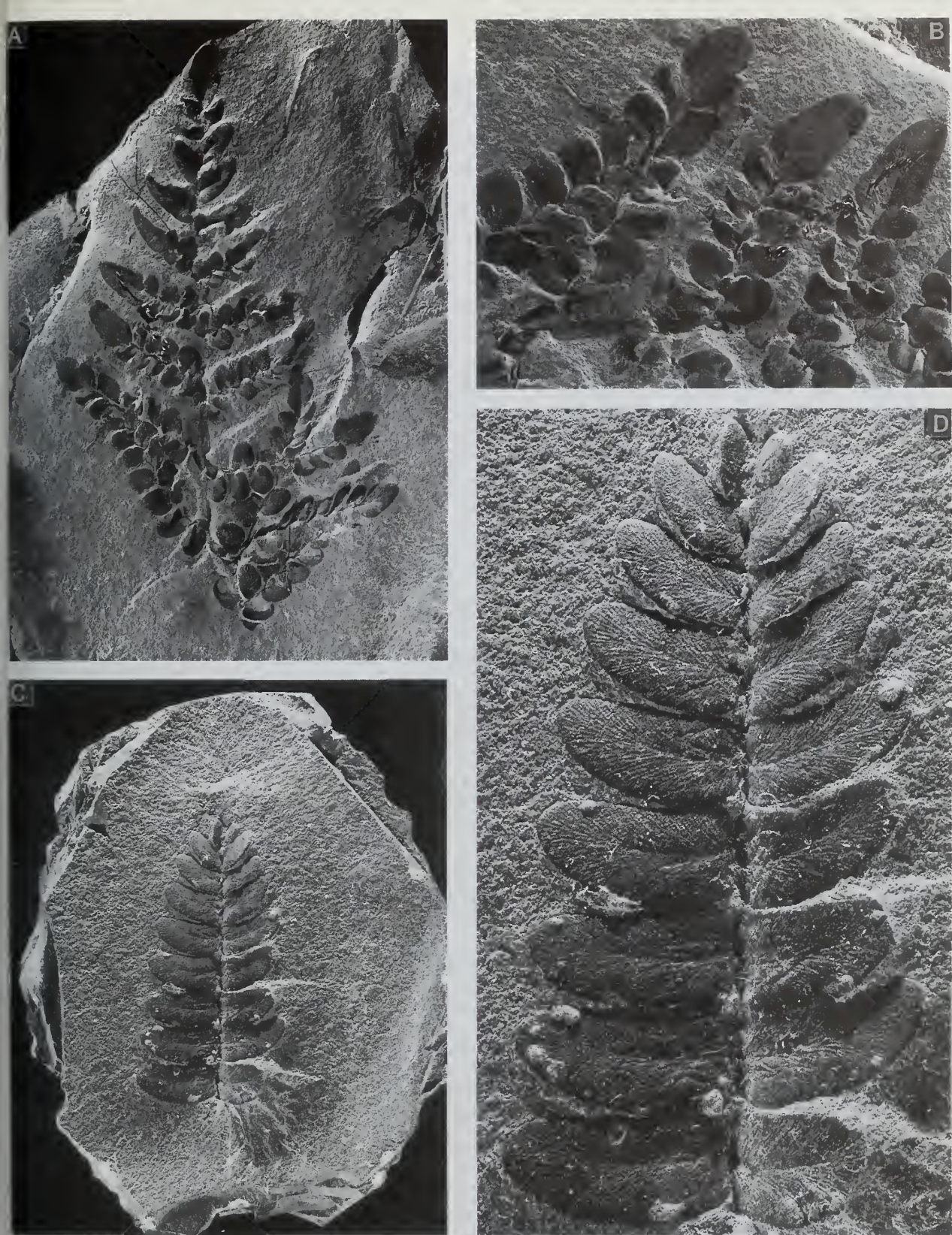


fig. 13 *Neuropteris obliqua* (Brongniart) Zeiller. V.63723. Duckmantian (Westphalian B), Rhigos, near Hirwaun, Mid-Glamorgan, UK. A, whole specimen, $\times 1$. B, enlargement of pinnules, $\times 2$. *Paripteris pseudogigantea* (Potonié) Gothan. V.63724. Duckmantian (Westphalian B), Rhigos, near Hirwaun, Mid-Glamorgan, UK. C, whole specimen, $\times 1$. D, enlargement of pinnules, $\times 3$.



Fig. 14 *Neuropteris obliqua* (Brongniart) Zeiller. Duckmantian (Westphalian B), Yorkshire, UK. Photograph taken in the field of the proximal portion of a frond preserved in sandstone. Previously illustrated at lower magnification by Scott (1978: pl. 27, fig. 1). A, whole specimen, $\times 0.2$. B, pinnate foliage from above dichotomy, $\times 0.5$. C, pinnae attached to primary rachis below the dichotomy, $\times 1$.

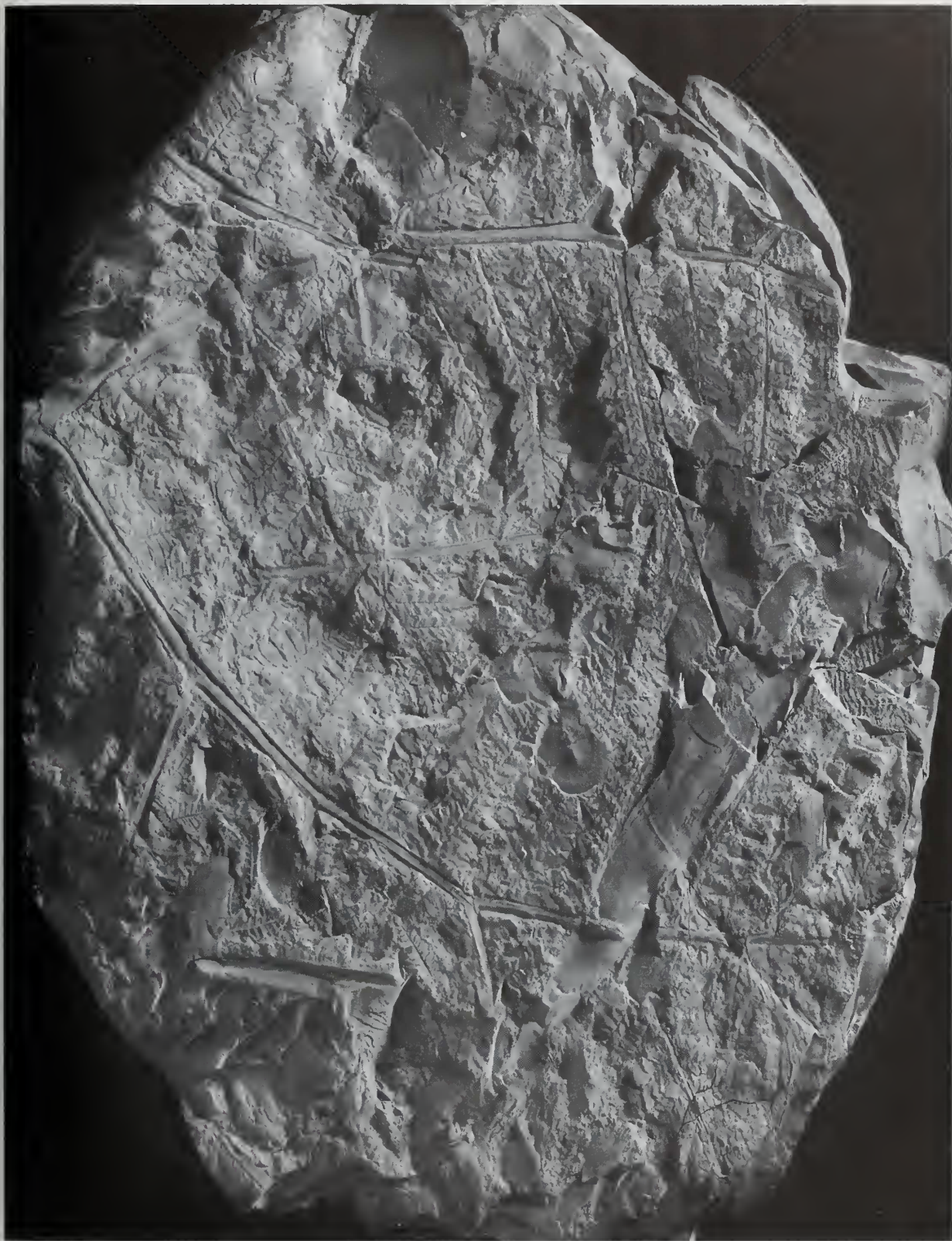


fig. 15 *Neuropteris heterophylla* (Brongniart) Sternberg. V.1797. Duckmantian (Westphalian B), Clay Cross, Derbyshire, UK. $\times 0.34$.

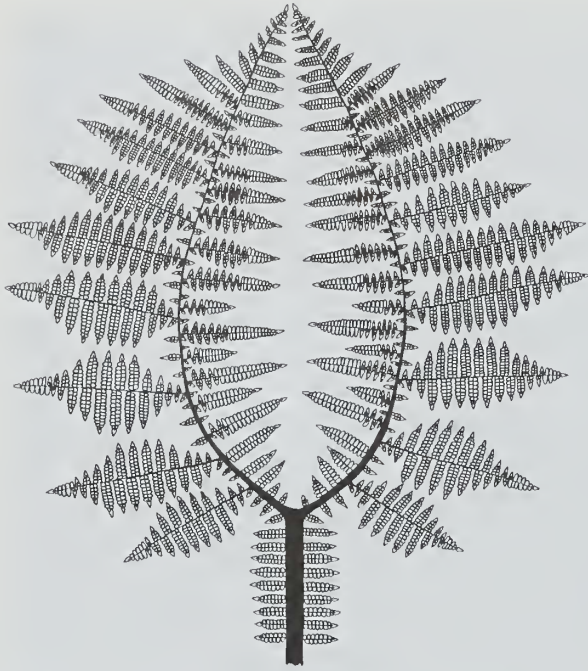


Fig. 16 Reconstruction of *Neuropteris* frond (*N. heterophylla* (Brongniart) Sternberg). From Cleal & Shute (1991: fig. 29).

In his investigations on Stephanian plant fossils from the Caucasus, Shchegolev (1979) described some fragments of neuropteroid fronds, which also had relatively large, lax-limbed pinnules and wide venation, and for which he proposed the new name *Sphenoneuropteris*. We still have very little information on the architecture of these fronds, and nothing of the epidermal structure or fructifications. It is far from clear, therefore, whether this is a homogeneous group of species. However, for the time being *Sphenoneuropteris* provides a convenient receptacle for these distinctive frond fragments, which clearly have little to do with *Neuropteris sensu stricto*, or probably even the Trigonocarpaceae in general.

SYSTEMATICS

Form-genus *LAVEINEOPTERIS* Cleal, Shute & Zadow

Laveineopteris guadiatensis (Wagner) Cleal & Shute, comb. nov.

*1983b *Neuropteris guadiatensis* Wagner: 95; pl. 1.

REASON FOR GENERIC ASSIGNMENT. Wagner records associated orbicular cyclopterid pinnules with the more typical pinnate foliage of this species. Also, fragmentary cuticles prepared by C.R. Hill (Natural History Museum) and shown to us, display a number of laveineopterid characteristics: adaxial cuticle shows relatively uniform cell patterns, no anticlinal walls preserved on abaxial cuticle, and no trichomes are preserved on either cuticle.

OCCURRENCE. S. Spain (Duc).

Laveineopteris hollandica (Stockmans) Cleal & Shute, comb. nov.

* 1933 *Neuropteris hollandica* Stockmans: 31–34; pl. 10, fig. 1.

v 1959 *Neuropteris rytoniana* Kidston ex Crookall: 113–114; pl. 52, figs 3–4; pl. 54, fig. 1 (vide Laveine, 1967).

.v 1959 *Neuropteris formosa* Kidston ex Crookall: 139–140; pl. 52, figs 1–2.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule morphology with *L. tenuifolia*.

COMMENTS. Although its venation is not entirely typical, *N. formosa* is taken to be a later synonym of *L. hollandica* based on the similarity in shape of its subtriangular pinnules. Also, the types of *N. formosa* originated from the same locality as the types of *N. rytoniana*, which Laveine (1967) assigned to *L. hollandica*.

OCCURRENCE. Pennines (Lan-Bol), Franco-Belgian Basin (Lan-Duc), S. Limburg (Lan), NW Germany (Lan-Bol), NE Germany (Lan-Bol).

Laveineopteris jongmansii (Crookall) Cleal & Shute, comb. nov.

v? 1888 *Neuropteris plicata* Sternberg; Kidston: 313; pl. 1, fig. 1.

? 1917 *Neuropteris subplicata* Kidston: 1031.

*v 1959 *Neuropteris jongmansii* Crookall: 178; pl. 51, fig. 1.

.v 1967 *Neuropteris chaldardi* Laveine: 176–181; pls 35–39.

REASON FOR GENERIC ASSIGNMENT. Great similarity of pinnule morphology to *L. tenuifolia*.

COMMENTS. Laveine (1967) noted the close similarity between his *N. chaldardi* and the holotype of *L. jongmansii* figured by Crookall (1959). Crookall's specimen alone was inadequate evidence for Laveine to make a proper comparison. However, one of us (CJC) has examined additional material in the collections of the British Geological Survey and can confirm that the two species are identical.

The type and only known specimen of *N. subplicata* has similar shaped pinnules and a dense venation. The apical pinnule is rather small, but can be compared with the lower end of the range of variation of *L. jongmansii* (e.g. Laveine 1967: pl. 37, fig. 2). More examples of this species are needed but, if the synonymy can be confirmed, Kidston's species will be the valid name.

OCCURRENCE. Pennines (Bol), Franco-Belgian Basin (Bol), NW Germany (Bol), Lublin (Bol), NE Germany (Bol).

Laveineopteris loshii (Brongniart) Cleal, Shute & Zadow

* 1831 *Neuropteris Loshi* Brongniart: 242; pl. 72, fig. 1; pl. 73.

.v 1959 *Neuropteris hemingwayi* Crookall: 121–122; pl. 46, fig. 6.

T 1967 *Neuropteris loshi* Brongniart; Laveine: pls C–D.

§ 1990 *Laveineopteris loshii* (Brongniart) Cleal, Shute & Zadow: 490.

REASON FOR GENERIC ASSIGNMENT. Type species.

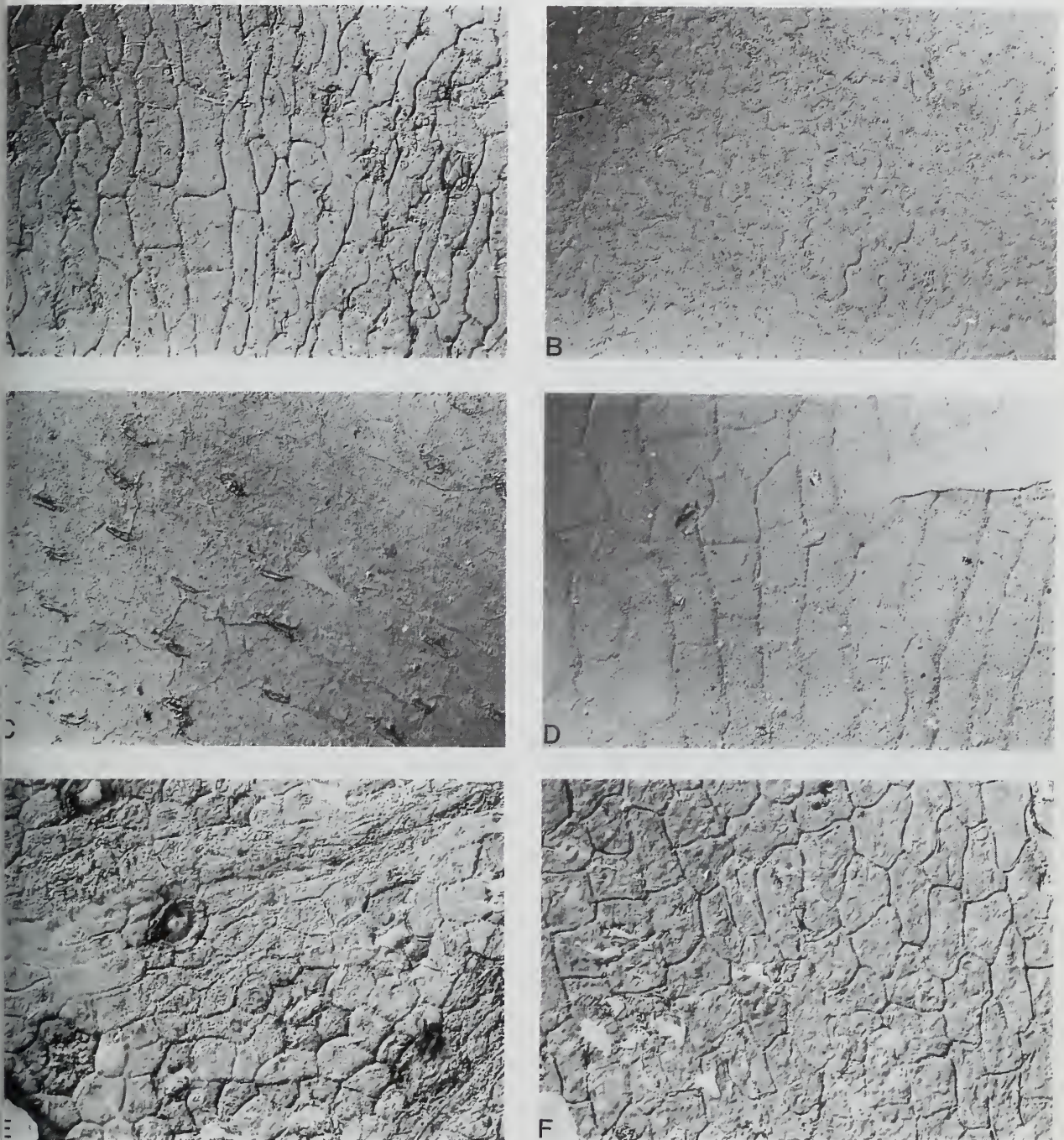


fig. 17 Neuropteroid cuticles photographed using Normarski Interference. All $\times 200$. A, *Neuropteris ovata* Hoffmann. Abaxial cuticle. V.62925. Basal Westphalian D, Kallenberg Seam, Itzenplitz Colliery, Saarland, Germany. B, *N. ovata*. Adaxial cuticle. V.62924. Same horizon and locality. C, *Laveineopteris loshii* (Brongniart) Cleal *et al.*. Abaxial cuticle. V.62974. Duckmantian (Westphalian B), Royosborn Colliery Borehole, North Yorkshire, UK. D, *L. loshii*. Adaxial cuticle. V.62948. Same horizon and locality. E, *Macroneuropteris macrophylla* (Brongniart) Cleal *et al.*. Abaxial cuticle. V.62295. Upper Westphalian D, Upper Bonnar Seam, Brogan's Pit, Sydney Coalfield, Cape Breton, Canada. F, *M. macrophylla*. Adaxial cuticle. V.63055. Same horizon and locality.

COMMENTS. The epidermal structure has been described by Cleal & Shute (1992) and orbicular cyclopterid pinnules have been shown attached near the base of its frond (von Roehl 1868: pl.17).

N. hemingwayi was based on a single fragment from the Parkgate Coal (upper Langsettian) of Yorkshire, from which *L. loshii* is well documented (e.g. Crookall 1959: pl.28, fig.4). It is poorly preserved, but the pinnule shape and venation seem indistinguishable from *L. loshii*.

OCCURRENCE. South-West UK (Lan-Bol), Pennines, UK (Lan-Bol), Franco-Belgian Basin (Lan-Bol), S. Limburg (Lan), NW Germany (Lan-Bol), NE Germany (Lan-Bol), Lublin (Lan-Bol), Intra-Sudetic Basin (Duc-Bol), U. Silesia (Lan-Bol), Svoge (Duc-Bol), Donets (Lan-Duc).

Laveineopteris morinii (Bertrand ex Laveine) Cleal & Shute, comb. nov.

* 1967 *Neuropteris morinii* Bertrand ex Laveine: 227–228; pls 63–65.

REASON FOR GENERIC ASSIGNMENT. The association of orbicular cyclopterid pinnules (Laveine 1967: pl. 64 fig. 6), and general similarity of some of the pinnules to the more elongate-pinnule laveineopterids such as *L. tenuifolia* and *L. hollandica*.

COMMENTS. Laveine (1967) argued that this species belongs to the general group allied to *Neuropteris obliqua*, and would thus be retained in *Neuropteris* in its restricted sense as used here. This was based mainly on the supposed presence of forma *impar*-type pinnules. However, the best example that he illustrates to justify this opinion (Ibid. pl. 65 fig. 5) is poorly localized and there is no evidence that it was associated with more typical pinnules of this species. The other two examples (Ibid. pl. 63 figs 2–3), although in clear association with specimens showing the more typical pinnule form of this species, are isolated pinnules – one possibly a terminal, the other a lateral. Being isolated, it is far from certain that they are of the forma *impar* type from the lower part of a frond, or even that they belong to the same species.

It is true that the cyclopterid illustrated by Laveine is also only associated with the specimens of pinnate foliage. However, in view of the close similarity of the pinnules to *L. tenuifolia* (from which it can only be reliably distinguished by its denser, occasionally flexuous veins), we believe that the association with the cyclopterid reflects an original organic connection.

OCCURRENCE. Franco-Belgian Basin (Bol).

Laveineopteris nicolausiana (Gothan) Cleal & Shute, comb. nov.

* 1913 *Neuropteris nicolausiana* Gothan: 213; pl. 48; pl. 49, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The similarity of the pinnule shape to *L. rarinervis* and of the venation to *L. tenuifolia*. Also, the frequent association of orbicular cyclopterids.

COMMENTS. Many authors have regarded this as indistinguishable from *L. rarinervis* (e.g. Stockmans 1933, Crookall 1959, Laveine 1967). However, it differs from that species in having (a) more linguaeform lateral pinnules, (b) lateral veins

that fork at a narrower angle and meet the pinnule margin at a more oblique angle, and (c) smaller, more ovoid apical pinnules. It is thus in some ways morphologically intermediate between typical *L. rarinervis*, and the larger-pinnuled species *L. tenuifolia*. In view of its stratigraphical occurrence at the lower end or just below the range of *L. rarinervis*, it is possible that it represents its evolutionary ancestor and a link with the larger-pinnuled *L. tenuifolia* group of species.

Bertand (1930) altered the spelling to *nikolausii*, changing it to the substantive form and reverting to the original spelling of the surname Nikolaus. However, ICBN Article 73 allows a species name to be based on an latinized personal name in an adjectival form. The original spelling is therefore retained.

OCCURRENCE. Intra-Sudetic Basin (Bol), U. Silesia (Duc-Bol), Saar-Lorraine (Duc-Bol).

Laveineopteris piesbergensis (Gothan) Cleal & Shute, comb. nov.

* 1953 *Imparipteris piesbergensis* Gothan: 57; text fig. 8; pl. 32.

REASON FOR GENERIC ASSIGNMENT. The presence of orbicular cyclopterids in the proximal part of the frond (Gothan 1953: text fig. 8), and the close similarity of the pinnules to *L. rarinervis*.

COMMENTS. Gothan distinguished this species from *L. rarinervis* by a number of characters of the orbicular cyclopterid pinnules, which are probably of doubtful taxonomic significance. However, he also mentioned that the venation of the lateral pinnules was denser and more oblique to the pinnule margin. The significance of these differences of veining pattern is not clear, and Laveine (1967) included Gothan's species in the synonymy of *L. rarinervis*. However, we have opted to maintain the distinction, at least until the German material can be more fully assessed.

OCCURRENCE. NW Germany (WeD).

Laveineopteris rarinervis (Bunbury) Cleal, Shute & Zodrow

Fig. 5

* 1847 *Neuropteris rarinervis* Bunbury: 425; pl.22.

[§]1990 *Laveineopteris rarinervis* (Bunbury) Cleal, Shute & Zodrow: 490.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Cleal & Zoderow 1989) and the presence of orbicular cyclopterid pinnules near the dichotomy of a bipartite frond (Laveine 1967: pl.45, fig.3).

OCCURRENCE. South-West UK (Bol-Can), Pennines (Bol-WeD), Franco-Belgian Basin (Bol-WeD), NW Germany (Bol-WeD), NE Germany (Bol), Lublin (Duc-Bol), U. Silesia (Bol-WeD), Donets (Duc-WeD), Turkey (WeD), (?)NW Spain (WeD).

Laveineopteris tenuifolia (Sternberg) Cleal, Shute & Zoderow

T 1820 *Filicites tenuifolius* Schlotheim: 405; pl. 22, fig. 1.

* 1825 *Neuropteris tenuifolia* Schlotheim ex Sternberg: xvii.

[§]1990 *Laveineopteris tenuifolia* (Sternberg) Cleal, Shute & Zoderow: 490.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962, Cleal 1985). Also, pinnate fragments of this species are almost invariably associated with orbicular cyclopterid pinnules.

COMMENTS. This species has been widely reported from the Iberian Peninsula. However, Cleal (1981) analysed these records and showed that they were based either on specimens of *Neuropteris resobae* Cleal (q.v.), or on unidentifiable fragments; *L. tenuifolia* would seem to be absent from this area.

OCCURRENCE. South-West UK (Lan-WeD), Pennines (Lan-Bol), Franco-Belgian Basin (Lan-WeD), S. Limburg (Lan), NW Germany (Lan-WeD), Lublin (Lan-Bol), Intra-Sudetic Basin (Duc-Bol), U. Silesia (Lan-Bol), Saar-Lorraine (Bol), Svoge (Duc-Bol), Donets (Duc-WeD).

Form-genus *MACRONEUROPTERIS* Cleal, Shute & Zodrow

Macroneuropteris britannica (Gutbier) Cleal, Shute & Zodrow

- * 1835 *Odontopteris britannica* Gutbier: 68, pl. 9, figs 8–11.
- § 1990 *Macroneuropteris britannica* (Gutbier) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962).

OCCURRENCE. Zwickau-Oelsnitz (WeD).

Macroneuropteris macrophylla (Brongniart) Cleal, Shute & Zodrow Figs 6–7 17E–F

- * 1831 *Nevropteris macrophylla* Brongniart: 235; pl. 65, fig. 1.
- § 1990 *Macroneuropteris macrophylla* (Brongniart) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Cuticles have been described by Cleal & Zodrow (1989). The frond architecture is currently under review by Cleal, Laveine & Shute.

The specimens from North Caucasus illustrated by Anisimova (1979) as this species are clearly misidentified. They are isolated pinnules which resemble those of *Paripteris* (e.g. *P. pseudogigantea*), although they would seem to have originated from rather a high stratigraphical position (WeD) for that form-genus.

OCCURRENCE. South-West UK (WeD-Can)

Macroneuropteris scheuchzeri (Hoffmann) Cleal, Shute & Zodrow

- * 1827 *Neuropteris scheuchzeri* Hoffmann: 157; pl. 1b, figs 1–4.
- § 1990 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1961, Cleal & Zodrow 1989). The frond architecture is currently under review by Cleal & Laveine.

COMMENTS. Havlena (1953; pl. 5, fig. 3) figured a fragment

reputedly from the Stephanian C of the Intra-Sudetic Basin as *Neuropteris cordata*. He claimed similar material also occurred in the Autunian of this region. As pointed out by Laveine (1967), however, the figured specimen is almost certainly *M. scheuchzeri*. If it does belong there and its stated provenance is correct, this is by far the highest stratigraphical occurrence of this species in Europe.

OCCURRENCE. South-West UK (Duc-Can), Pennines (Lan-Bol), Franco-Belgian Basin (Duc-WeD), S. Limburg (Duc), NW Germany (Duc-WeD), NE Germany (Duc-Bol), Lublin (Bol), Intra-Sudetic Basin (Duc-WeD, ?StC-Aut), U. Silesia (Lan-Bol), Saar-Lorraine (Bol), Alps (Can), Svoge (Bol), Donets (Duc-WeD), N. Caucasus (WeD), Turkey (WeD), N. Portugal (WeD), NW Spain (WeD-Can), S. Portugal (WeD).

Macroneuropteris subauriculata (Sterzel) Cleal, Shute & Zodrow

- T 1855 *Neuropteris auriculata* Brongniart: Geinitz: pl. 27, figs 4–7, 9.
- * 1901 *Neuropteris subauriculata* Sterzel: 100.
- § 1990 *Macroneuropteris subauriculata* (Sterzel) Cleal, Shute & Zodrow: 488.

REASON FOR GENERIC ASSIGNMENT. Epidermal structure (Barthel 1962) and possibly frond architecture (Daber 1957).

COMMENTS. This species appears to be endemic to the Zwickau-Oelsnitz Basin. The record from North Caucasus by Anisimova (1979) is based on extremely poorly preserved material and is unconvincing.

Laveine (1989; pl. 60, fig. 1) has figured a single fragment of this species from the upper Westphalian D (or possibly basal Cantabrian) of Saar-Lorraine. It bears a close similarity to the fragmentary types of *Neuropteris germeri* de Jong, from slightly older strata in Saar-Lorraine, and which we have provisionally assigned to *N. ovata*. Cuticles from this Saar-Lorraine material could help resolve their taxonomic position.

OCCURRENCE. Zwickau-Oelsnitz (WeD).

Form-genus *MARGARITOPTERIS* Gothan

Margaritopteris multivenosa (Purkyňová) Cleal & Shute, comb. nov.

- * 1970 *Neuropteris multivenosa* Purkyňová: 223–224; pl. 45, fig. 1, pl. 46, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The prominent midvein and the size and texture of the pinnules (see Laveine *et al.* 1977). Also the manner of lobing of the pinnules.

COMMENTS. Laveine *et al.* (1977) were clearly of the opinion that this species belongs to *Margaritopteris*, and was the precursor of the more familiar Westphalian species, although no formal proposal of transference was made. The factors mentioned above, particularly well shown in Laveine *et al.* (1977, pl. 19, fig. 3), make it unnecessary to postpone the proposal of transference.

OCCURRENCE. U. Silesia (Alp).

Form-genus *NEURALETHOPTERIS* Cremer ex Laveine

Neuraethopteris densifolia Josten

- * 1983 *Neuraethopteris densifolia* Josten: 144; pl. 53, fig. 1; pl. 54, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The alethopteroid nature of the venation.

OCCURRENCE. NW Germany (Kin-Yea).

Neuraethopteris doubravica (Purkyňová) Cleal & Shute, comb. nov.

- * 1971 *Neuropteris doubravica* Purkyňová: 165–166; pls 6–9.

REASON FOR GENERIC ASSIGNMENT. The cordate base of the pinnules and the prominent midvein.

COMMENTS. The generic position of this species is far from certain. At least some of the specimens figured in the protologue, particularly those with smaller pinnules, approach *Neuropteris* in venation and pinnule shape (e.g. pl. 8, fig. 1a). As pointed out by Purkyňová, however, the larger pinnules share many characters with *Neuraethopteris*, especially *N. jongmansii*, and so we propose to transfer the species there.

OCCURRENCE. U. Silesia (Lan).

Neuraethopteris jongmansii Laveine

- * 1967 *Neuraethopteris jongmansii* Laveine: 107; pls 2–4.

REASON FOR GENERIC ASSIGNMENT. The typically alethopteroid nature of venation (Laveine 1967). Also, *Whittleseya* sporangial structures and *Trigonocarpus* ovules have been linked by Jongmans (1954) to foliage identified as *N. jongmansii* by Laveine (1967).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Lan), S. Limburg (Lan), NW Germany (Lan), U. Silesia (Lan).

Neuraethopteris larischii (Šusta) Laveine

- * 1930 *Neuropteris Larischi* Šusta: 5, pl. 1.
§ 1967 *Neuraethopteris larischi* (Šusta) Laveine: 102; pl. 1.

REASONS FOR GENERIC ASSIGNMENT. Typically alethopteroid nature of venation (Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Arn-Lan), NW Germany (Arn-Lan), U. Silesia (Kin-Lan), N. Caucasus (?Kin-Yea), Turkey (Yea), NW Spain (Lan).

Neuraethopteris neuropteroides (Šusta) Josten

- * 1927 *Alethopteris neuropteroides* Šusta: 4; pl. 1, fig. 2.
§ 1983 *Neuraethopteris neuropteroides* (Šusta) Josten: 138; pl. 50, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The close similarity in pinnule shape to *N. schlehanii*, and the tendency of the pinnules to be fused to the rachis at the base.

COMMENTS. This species seems to occupy a position intermediate between *Neuraethopteris* and true *Alethopteris*.

OCCURRENCE. Franco-Belgian Basin (Kin-Lan), NW Germany (Kin-Lan), U. Silesia (Yea-Lan).

Neuraethopteris rectinervis (Kidston) Laveine

- *v 1888 *Neuropteris rectinervis* Kidston: 314; pl. 1, figs 2–4.
T 1959 *Neuropteris Schlehani* forma *rectinervis* (Kidston) Crookall: 145–147; pl. 35, figs 6–8.
§ 1967 *Neuraethopteris rectinervis* (Kidston) Laveine: 120; pl. 9.

REASON FOR GENERIC ASSIGNMENT. typically alethopterid nature of venation (Laveine 1967).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Lan), NW Germany (Lan), U. Silesia (Lan), Donets (Lan).

Neuraethopteris schlehanii (Stur) Laveine Fig. 8

- * 1877 *Neuropteris Schlehani* Stur: 289; pl. 28, figs 7–8.
. 1953 *Neuropteris schlehanioides* Stockmans & Willière: 233; pl. 31, figs 3, 7; pl. 36, fig. 2.
.? 1953 *Neuropteris loriformis* Stockmans & Willière: 234; pl. 16, fig. 2.
. 1977 *Neuropteris rectinervis* forma *obtusata* Tenčov: 59–60; pl. 20, figs 3–4.
. 1977 *Neuropteris lata* Tenčov: 60; pl. 21, figs 2–3.
. 1977 *Neuropteris longifolia* Tenčov: 61; pl. 21, figs 4–9.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Epidermal structures have been described by Cleal & Shute (1992). Also, *Aulacotheca* sporangial structures were reported in close association with it by Laveine (1967: pl. 5, fig. 3).

The types of *N. schlehanioides* clearly represent fragments from high in the pinna of *N. schlehanii* and can be compared with parts of Laveine (1967: pl. 6, figs 2–3). The type of *N. loriformis* is less typical, having extremely long, slender pinnules. As pointed out by Stockmans & Willière (1953), however, it occurs in association with *N. schlehanii* and has a comparable venation pattern.

Neuropteris longifolia and *N. lata* were erected for specimens from the Svidnaya Formation of the Svoje Basin. The pinnules are rather large (up to 30 mm long), but are otherwise very similar to *N. schlehanii*, with which they are closely associated. As Laveine (1967: pl. 8) has figured specimens of *N. schlehanii* with pinnules approaching these in size, there seems little reason for separating these species.

Tenčov (1977) described the types of *N. rectinervis* forma *obtusata* as having a venation nearer to that of *N. rectinervis* than *N. schlehanii*. However, the veining is in fact quite compatible with *N. schlehanii*, being broadly arched (cf. Laveine 1967: pl. 7 fig. 1; pl. 8 fig. 4).

OCCURRENCE. South-West UK (Lan), Pennines (Lan), Franco-Belgian Basin (Pen-Lan), S. Limburg (Lan), NW Germany (Mrd-Lan), NE Germany (Kin-Lan), (?) Lublin (Kin-Yea), Intra-Sudetic Basin (Lan), U. Silesia (Alp-Lan), Svoje (Yea-Lan), Donets (Pen-Lan), N. Caucasus (?Kin-Lan), Turkey (Lan), Alps (Lan), Pyrenees (Kin), NW Spain (Lan).

Form-genus *NEUROCALLIPTERIS* Sterzel*Neurocallipteris gallica* (Zeiller) Cleal & Shute, comb. nov.

* 1888a *Neuropteris gallica* Zeiller: 248; pl. 29, figs 1–3.

REASON FOR GENERIC ASSIGNMENT. Close similarity to *N. planchardii* in both pinnule shape and venation.

COMMENTS. This species is not well documented, and it is not entirely certain that it is distinct from *N. planchardii*. As pointed out by Wagner (1963), many of the differences claimed by Zeiller may be merely a function of the position of the pinnules within a frond. The most obvious difference is the presence of hairs near the midvein of *N. gallica*, but this could be influenced by taphonomic factors. There have, however, been a number of records of the species in recent years, and so it has provisionally taken to be 'good'.

OCCURRENCE. Saar-Lorraine (Bar), Massif Central (StC), NW Spain (StB), S. Spain (StC), N. Portugal (StC).

Neurocallipteris neuropteroides (Göppert) Cleal, Shute & Zodrow Figs 9–10

* 1836 *Gleichenites neuropteroides* Göppert: 186; pls 4–5.

§ 1990 *Neurocallipteris neuropteroides* (Göppert) Cleal, Shute & Zodrow: 489.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Epidermal structure (Barthel 1962, 1976) and frond architecture (Barthel 1976, Šetlík 1980) have been documented for this species.

OCCURRENCE. Saxony (Aut), Intra-Sudetic Basin (StB-Aut), Massif Central (StC), Pyrenees (StC), NW Spain (StC), N. Portugal (StC-Aut).

Neurocallipteris planchardii (Zeiller) Cleal, Shute & Zodrow

* 1888a *Neuropteris planchardii* Zeiller: 246; pl. 28, figs 8–9.

§ 1990 *Neurocallipteris planchardii* (Zeiller) Cleal, Shute & Zodrow: 489.

REASON FOR GENERIC ASSIGNMENT. Similarity of epidermal structures to *N. neuropteroides* (see Reichel & Barthel 1964, Barthel 1976).

OCCURRENCE. Saxony (Aut), Intra-Sudetic Basin (Aut), N. Caucasus (StC), Alps (?Can), Massif Central (StB-Aut), Pyrenees (StC), NW Spain (WeD-StB), N. Portugal (StC-Aut).

Form-genus *NEURODONTOPTERIS* Potonié*Neurodontopteris auriculata* (Brongniart) Potonié Figs 11–12

† 1830 *Nevropteris auriculata* Brongniart: pl. 36.

1831 *Nevropteris auriculata* Brongniart: 236.

1831 *Neuropteris dufrenoyi* Brongniart: 246.

1893 *Neurodontopteris auriculata* (Brongniart) Potonié: 124.

.(?)1937 *Neuropteris densinervosa* (Grigoriev) Zalesky: 183; fig. 31.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. There have been no descriptions of cuticles under this species name. However, Z. Šimunek (pers. comm. 1992) has shown that cuticles described by Barthel (1976) as *Neuropteris cordata* in fact belong to *Neurodontopteris auriculata*. In contrast to typical *N. cordata* from the Massif Central, the specimens which yielded the cuticles have smaller pinnules (<60 mm long) with a rounder apex, and a denser venation (30 veins per cm on the pinnule margin). Šimunek has prepared very similar cuticles from specimens of *N. auriculata* from the Intra-Sudetic Basin, examples of which are shown in Fig. 11.

The inclusion of *N. densinervosa* here must be regarded as tentative, since only two specimens have been illustrated in the literature and one of those (the holotype) only as a drawing. However, the large pinnules and high stratigraphical position (Gzhelian) of the specimens would seem compatible with *N. auriculata*.

OCCURRENCE. Saar-Lorraine (Aut), Saxony (Aut), Intra-Sudetic Basin (StB-Aut), NW Spain (StB), S. Spain (StC-Aut).

Form-genus *NEUROPTERIS* (Brongniart) Sternberg*Neuropteris antecedens* Stur

* 1875 *Neuropteris antecedens* Stur: 53; pl. 15, figs 1–6.

. 1953 *Neuropteris mathieuvi* Stockmans & Willière: 227.

. 1955 *Neuropteris condrusiana* Stockmans & Willière: 12; pl. 6, figs 1–7, 9–15; pl. 9, figs 1–8.

. 1955 *Neuropteris papilioniformis* Stockmans & Willière: 13; pl. 2, fig. 3.

. 1955 *Neuropteris pseudozamites* Stockmans & Willière: 13, pl. 2, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The tendency of the pinnules to be broadly attached to the rachis and on the venation sometimes being flexuous (Crookall 1959).

COMMENTS. The type of *N. mathieuvi* was found associated with typical specimens of *N. antecedens*, and it is difficult to see why it is not merely the small-pinnuled form of that species.

The types of *N. condrusiana*, *N. papilioniformis* and *N. pseudozamites* all originated from the same horizon and locality, and were associated with a specimen which Stockmans & Willière (1955) identified as their *N. mathieuvi*. All of this material clearly belongs to a single species, and bears quite a striking similarity to the types of *N. antecedens*; it in fact represents one of the best documentations in the literature of the morphological variability of that species.

OCCURRENCE. South-West UK (Arn), Pennines (Asb-Arn), Franco-Belgian Basin (Pnd-Arn), U. Silesia (Asb-Arn), Svoge (?Arn).

Neuropteris bohdanowiczii (Zalesky) Gothan

* 1907 *Sphenopteris bohdanowiczi* Zalesky: 33, 65; pl. 2, fig. 2.

- § 1913 *Neuropteris bohdanowiczi* (Zalessky) Gothan: 210; pl. 44, fig. 4; pl. 53, fig. 1.

REASON FOR GENERIC ASSIGNMENT. The relatively weakly developed midvein, the slightly flexuous lateral veins, and the tendency of the pinnules to be fused to the rachis.

COMMENTS. This is a relatively poorly known species, the best documented records being by Gothan (1913) and Kota-sowa (1968). Zalessky (1907) suggested that it should be placed in a new subgenus, *Sphenopteris* subg. *Neurosphenopteris*. However, it is doubtful if the latter is validly published according to the ICBN (Danzé 1956).

OCCURRENCE. U. Silesia (Alp).

Neuropteris ervedosensis (Teixeira) Wagner

- * 1942 *Mixoneura ervedosensis* Teixeira: 8; pl. 1.
§ 1963 *Neuropteris ervedosensis* (Teixeira) Wagner: 27.

REASON FOR GENERIC ASSIGNMENT. The apparent occurrence of enlarged, 'forma impar'-like pinnules in the lower part of the frond. Also, the veining, although rather less dense, has some resemblance to that of *N. ovata* and *N. flexuosa*.

COMMENTS. Opinion is divided as to the affinities of this species. De Jong (1974) regards it as being closely related to *N. ovata*, while Wagner & Sousa (1983) state that there is probably no relation with this species or *N. flexuosa*. As stated above, its affinities seem to lean towards *Neuropteris*, particularly as it probably has enlarged pinnules low in the frond, but this must be taken as provisional, at least until better information on the frond architecture becomes available.

OCCURRENCE. N. Portugal (WeD).

Neuropteris flexuosa Sternberg

- T 1823 *Osmunda gigantea*, var. β Sternberg: pl. 32, fig. 2.
* 1825 *Neuropteris flexuosa* Sternberg: xvi.
T 1959 *Neuropteris ovata* Hoffmann, forma *flexuosa* (Sternberg) Crookall: text-fig. 52.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Cleal & Zodrow 1989) and close similarity of pinnule form to *N. ovata*.

COMMENTS. The European records of this species, other than those in Britain, are misidentifications of species such as *Laveineopteris tenuifolia* (e.g. Novik 1952, 1954) and *L. jongmansii* (e.g. Corsin 1932).

OCCURRENCE. South-West UK (WeD-Can), S Portugal (WeD).

Neuropteris ghayei Stockmans & Willière

- T 1933 *Neuropteris grangeri* Brongniart; Stockmans: pl. 12, fig. 3.
* 1954 *Neuropteris ghayei* Stockmans & Willière in Pastiels & Willière: 59.

REASON FOR GENERIC ASSIGNMENT. Underlying similarity in pinnule form with *N. heterophylla* and *N. obliqua*. Also, on the presence of large 'impar'-type pinnules (Laveine 1967: pl. 49, fig. 5), similar to those found in the lower part of the *N. obliqua* frond.

OCCURRENCE. Franco-Belgian Basin (Lan), NW Germany (Lan)

Neuropteris heterophylla (Brongniart) Sternberg Figs 15–16

- * 1822 *Filicites* (*Neuropteris*) *heterophyllus* Brongniart: 239; pl. 2, fig. 6.
§ 1825 *Neuropteris heterophylla* (Brongniart) Sternberg: xvi.
T 1831 *Neuropteris* (*sic*) *heterophylla* Brongniart: pl. 71 (neotype – vide Laveine, 1967).
T 1967 *Neuropteris heterophylla* Brongniart (*sic*); Laveine: pl. A.

REASON FOR GENERIC ASSIGNMENT. Type species.

COMMENTS. Both epidermal structures and frond architecture have been documented by Cleal & Shute (1991a). Specimens of this species have sometimes been recorded as *Neuropteris grangeri* Brongniart (see comments by Laveine 1967).

The specimens from the Donets that have been illustrated in the literature as *N. heterophylla* appear to be misidentified specimens of *Laveineopteris loshii* (Novik 1952: pl. 61, figs 1–4; 1954: pl. 20, figs 5–6). However, Fissuneneko and Laveine (1984) claim that true *N. heterophylla* occurs here and, in view of Laveine's familiarity with the type specimens, the record has been accepted.

OCCURRENCE. Pennines (Duc), Franco-Belgian Basin (Lan-Bol), NW Germany (Lan-Bol), U. Silesia (Lan-Duc), Donets (Yea-WeD).

Neuropteris obliqua (Brongniart) Zeiller Figs 13A–B, 14

- T 1833 *Pecopteris obliqua* Brongniart: pl. 96, figs 1–4.
* 1834 *Pecopteris obliqua* Brongniart: 320–321.
§ 1888b *Neuropteris obliqua* (Brongniart) Zeiller: 284–289.
1953a *Neuropteris marginenervis* Jongmans: 15; pl. 5, figs 29–30; pl. 6, figs 31–32 (vide Laveine, 1967).
.v 1959 *Neuropteris lanarkiana* Kidston ex Crookall: 174; pl. 50, figs 1–2.
T 1967 *Neuropteris obliqua* (Brongniart) Zeiller; Laveine: pl. E, figs 1–2.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Cleal & Shute 1992) and frond architecture (Fig. 13; Gothan 1953: fig. 7; Scott 1978: pl. 27, fig. 1).

COMMENTS. The frond architecture of this species has still to be fully documented, but the available evidence suggests that it was essentially similar to that of *N. heterophylla*, except that the pinnules at the base of the frond were rather larger (the so-called 'forma impar'-type – e.g. Crookall (1959: pl. 47, fig. 4).

Crookall (1959) distinguished *N. lanarkiana* from *N. obliqua* by its more slender, triangular and widely-spaced pinnules, and less dense and straighter veins. However, such pinnules are not atypical in the *N. obliqua* fronds, and can be compared with a specimen figured by Laveine (1967: pl. 50, fig. 1a).

Stockmans & Willière (1965: pl. 3, fig. 8; pl. 5, figs 1–2) document specimens from NW Spain as this species, and Laveine (1967) has agreed with the identity of at least some of

them. However, the specimens are very fragmentary and, on their own, are inadequate for identification. There are no better documented specimens of this species from the Iberian Peninsula (the records by Wagner & Bowman 1983 and Alvarez-Vázquez in Wagner 1990 are unillustrated).

OCCURRENCE. South-West UK (Lan-Duc), Pennines (Lan-Bol), Franco-Belgian Basin (Mrd-Bol), S. Limburg (Lan-Duc), NW Germany (Mrd-Bol), NE Germany (Yea-Bol), Lublin (Lan-Bol), U. Silesia (Yea-Bol), Intra-Sudetic Basin (Lan), Svoge (Lan), Donets (Yea-Bol), N. Caucasus (?Kin-Lan), Turkey (Yea-Duc), Alps (Lan-Alps), S. Spain (Duc).

Neuropteris ovata Hoffmann

Fig. 17A–B

- * 1826 *Neuropteris ovata* Hoffmann: 266.
- T 1827 *Neuropteris ovata* Hoffmann: pl. 1b, fig. 6 (vide Satzwedel, 1969).
- . 1888a *Nevropteris stipulata* Zeiller: 255; pl. 29 fig. 5 (tentatively suggested by Wagner & Alvarez-Vázquez, 1991).
- p 1960 *Neuropteris valdensis* (Heer) Jongmans: 57; pl. 18, fig. 117.
- T 1969 *Imparipteris ovata* (Hoffmann) Gothan; Satzwedel: pl. 24 figs 1–2.
- v 1973 *Mixoneura polyneura* Doubinger & Germer: 50–51; pl. 1, fig. 2.
- ? 1974 *Neuropteris germeri* de Jong: 58; pls 21–22.
- v 1975a *Neuropteris pilosa* Doubinger & Germer: 18; pl. 7, fig. 1.

REASON FOR GENERIC ASSIGNMENT. Epidermal structures (Barthel 1962, Cleal 1985, Cleal & Zodrow 1989) and frond architecture (Zodrow & Cleal 1988).

COMMENTS. Cleal & Zodrow (1990) recognize varieties of this species, based partly on differences in epidermal structure. Also, Wagner (1963) assigns most of the Stephanian examples of the species to a separate variety (var. *grandeuryi* Wagner), based on the lateral veins being denser and less oblique to the pinnule margin. While recognizing that these varieties almost certainly have some biological validity, they will not be separated in this analysis.

The identity of upper Stephanian C specimens from north Portugal, described by Wagner & Sousa (1983) as *Neuropteris ovata* var. *pseudovata* Gothan & Sze, centers on one of the most contentious issues concerning the taxonomy of this species, viz. the difference between it and *Neurocallipteris neuropteroides*. There have been many analyses of this problem, the most detailed being by Zalesky (1909), Barthel (1976), Šetlík (1980) and Wagner & Sousa (1983). Šetlík and Wagner & Sousa have shown there are certain very subtle differences in pinnule form, but without the evidence of cuticles it is far from certain that they would be regarded as sufficient justification for separating them as species, let alone in different form-genera. It would seem that two quite separate groups of trigonocarpaleans have developed analogously similar pinnule morphologies, perhaps in response to similar environmental pressures. Consequently, identifying specimens with this type of pinnule in the upper Stephanian, if epidermal characters are unknown, is very difficult, if not impossible. Wagner & Sousa's Portuguese specimens have some of the characters (somewhat subtriangular pinnules, veins slightly oblique to pinnule margin) that tend to be commoner in *N. neuropteroides* than *N. ovata*. We have

therefore provisionally transferred their specimens to *N. neuropteroides*. However, we recognize that this needs to be confirmed by epidermal evidence or, if this is impractical, by larger specimens showing the form of the intercalated pinnules (cf. Šetlík 1980).

M. polyneura and *N. pilosa* were separated from *N. ovata* on minor characters of venation and surface detail, and their distinction cannot be maintained (Cleal 1985). *N. germeri*, which was described mainly on just two specimens, has a veining pattern and pinnule shape compatible with the larger forms of *N. ovata*, especially those of the var. *sarana* as described by Cleal & Zodrow (1989). The veining density is a little lower than is typical, but can probably be accommodated within the lower end of the range of variation. As the types of *N. germeri* are associated with more typical fragments of *N. ovata* var. *sarana* (Bertrand) Cleal & Zodrow, there seems little reason for distinguishing them taxonomically.

The type of *N. stipulata* is strikingly similar to *N. ovata* in pinnule shape, being relatively squat, having a basiscopic auricle and a short midvein. If Zeiller's drawing of the type of *N. stipulata* is accurate, the vein density is c.40 veins per cm, which is compatible with the form of *N. ovata*, normally found in the Stephanian, and known as var. *grandeuryi* Wagner.

OCCURRENCE. South-West UK (WeD-Can), Pennines (WeD), Franco-Belgian Basin, (WeD), NW Germany (WeD), U. Silesia (WeD), Saar-Lorraine (WeD), Donets (?Bol-?Bar), N. Caucasus (WeD, StB), Turkey (WeD), Alps (WeD-StC), Massif Central (Bar-StB, ?StC), NW Spain (WeD-StB), S. Spain (StC).

Neuropteris parvifolia Stockmans

- * 1933 *Neuropteris parvifolia* Stockmans: 28–29, pl. 8, figs 1–5.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule morphology and underlying venation pattern to *N. obliqua* (see Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), NE Germany (Duc-Bol), Lublin (Duc-Bol), Alps (Bol).

Neuropteris plicata Sternberg

- * 1833 *Neuropteris plicata* Sternberg: 70; pl. 19, figs 1,3.

REASON FOR GENERIC ASSIGNMENT. Close similarity of the pinnules to *N. ovata*.

COMMENTS. This is so similar to *N. ovata* that it is far from certain that it is a distinct species. Although Šetlík (1921) attempted an analysis of the morphological variation of the pinnules, the results were equivocal on this point. If they are the same species, then Sternberg's species would take priority. In view of the important palaeobotanical and biostratigraphical role played by *N. ovata*, a more thorough analysis of *N. plicata* should be undertaken before any nomenclatural changes are proposed.

OCCURRENCE. Intra-Sudetic Basin (WeD).

Neuropteris praeovata (Němejč) Cleal & Shute, comb. nov.

- * 1949 *Mixoneura praeovata* Němejč: 17–18; text fig. 2; pl. 4, figs 1–7.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule shape and venation to *N. ovata*.

COMMENTS. As pointed out by Němejč, this clearly belongs to the group of neuropterids allied to *N. ovata*, from which it can be reliably distinguished only by the more prominent midvein. Also, it is the only known member of this group of species to occur below the Westphalian D.

OCCURRENCE. Intra-Sudetic Basin (Bol).

Neuropteris resobae Cleal

- * 1981 *Neuropteris resobae* Cleal: 79, pls 1–2.

REASON FOR GENERIC ASSIGNMENT. Dense venation with relatively weak midvein. Pinnule limb often partly fused to rachis, and with basisopic auricle.

COMMENTS. Little is known of the frond architecture, other than that the ultimate pinnulae are terminated by a single apical pinnule, and nothing of the epidermal structures. Its retention in this form-genus is thus based entirely on pinnule morphology and venation, which clearly cannot be conclusive. The only other (albeit negative) piece of evidence is that, despite the size of the collection on which the species was described, not a single cyclopterid pinnule was found in association.

OCCURRENCE. NW Spain (Duc-WeD).

Neuropteris schaeferi Doubinger & Germer

- * 1975a *Neuropteris schaeferi* Doubinger & Germer: 10–11; pl. 4, fig. 1.

REASON FOR GENERIC ASSIGNMENT. Similarity of epidermal structure to *N. ovata* (see Saltzwedel 1968).

COMMENTS. This species is not really adequately documented, as only one small specimen has been described in the literature. However, in view of the epidermal evidence presented by Saltzwedel (1968), it has been included in the present analysis.

OCCURRENCE. Saar-Lorraine (StB).

Neuropteris semireticulata Josten

- * 1962 *Neuropteris semireticulata* Josten: 39–40; pl.3, figs 2–5.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule morphology and underlying venation pattern to *N. obliqua* (see Josten 1962).

OCCURRENCE. South-West UK (Duc-Bol), Pennines (Duc), Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), Lublin (Bol).

Neuropteris willierei Laveine

- * 1967 *Neuropteris willierei* Laveine: 224–227; pl.62.

REASON FOR GENERIC ASSIGNMENT. It is almost indistinguishable from *N. parvifolia*, differing only in having smaller, more broadly attached pinnules, and occurring stratigraphically lower (Laveine 1967).

OCCURRENCE. Franco-Belgian Basin (Lan-Duc), NW Germany (Lan-Duc).

Form-genus *PARIPTERIS* Gothan

Paripteris gigantea (Sternberg) Gothan

- * 1821 *Osmunda gigantea* Sternberg: 33; pl.22.
 § 1941 *Paripteris gigantea* (Sternberg) Gothan: 427.
 T 1953 *Neuropteris gigantea* Sternberg; Havlena: pl. 4; pl. 5, fig. 2.
 .v 1959 *Neuropteris maltbyensis* Crookall: 164; pl. 33, figs 7–8.
 ? 1965 *Paripteris veeni* Stockmans & Willièvre: pl. 2, figs 4–7 (vide Wagner & Bowman 1983).

REASON FOR GENERIC ASSIGNMENT. Type species.

OCCURRENCE. South-West UK (Lan-Duc), Pennines (Lan-Duc), Franco-Belgian Basin, (Mrd-Duc), NW Germany (Mrd-Bol), NE Germany (Kin-Lan), Lublin (Kin-Duc), Intra-Sudetic Basin (Lan-Bol), U. Silesia (Mrd-Bol), Svoge (Yea-Lan), Donets (Kin-Duc), N. Caucasus (?Kin-Lan), Turkey (Lan), Alps (Lan), Pyrenees (Kin), NW Spain (Mrd, Lan), S. Spain (Lan).

Paripteris linguaefolia (Bertrand) Laveine

- * 1930 *Neuropteris linguaefolia* Bertrand: 31–32; pl. 15.
 § 1967 *Paripteris linguaefolia* (Bertrand) Laveine: 266–267; pls 77–78.

REASON FOR GENERIC ASSIGNMENT. Frond architecture.

OCCURRENCE. Franco-Belgian Basin (Duc-Bol), NW Germany, (Bol), Lublin (Duc-Bol), Intra-Sudetic Basin (Duc-Bol), Saar-Lorraine (Duc-Bol), Donets (Duc-WeD), Turkey (Duc), Alps (Duc-Bol), NW Spain (Duc), S. Spain (Duc).

Paripteris linguaenova (Bertrand) Cleal & Shute, comb. nov.

- * 1930 *Neuropteris linguaenova* Bertrand: 29; pls 13–14.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule shape and venation to *P. linguaefolia*.

COMMENTS. Laveine (1967) assigned the types of this species to *P. pseudogigantea*. However, they are significantly larger (many are longer than 4 cm), have a thinner midvein, and lateral veins that diverge from the midvein at a narrower angle. More problematic is its distinction from *P. linguaefolia*. Bertrand (1930) separated them because *P. linguaefolia* has virtually no midvein, and 'la disposition et l'aspect des nervures sont très différents. . .'. As the types of *P. linguaenova* occur within the stratigraphical range of *P. linguaefolia*, these differences really need to be re-examined more critically. For the time being, however, the separation has been retained.

OCCURRENCE. Saar-Lorraine (Bol).

***Paripteris pseudogigantea* (Potonié) Gothan** Fig. 13C–D

- * 1897 *Neuropteris pseudogigantea* Potonié: 113; text fig. 102.
- 1941 *Neuropteris scheuchzeri* forma *minor* Novik: 457; pl. 22, fig. 2.
- * 1953 *Paripteris pseudogigantea* (Potonié) Gothan: 63–64; pl. 37, figs 1–4.

REASON FOR GENERIC ASSIGNMENT. Frond architecture (Laveine 1967: pls 73–76).

OCCURRENCE. South-West UK (Duc-Bol), Pennines (Duc-Bol), Franco-Belgian Basin (Duc-Bol), NW Germany (Duc-Bol), NE Germany (Duc-Bol), Lublin (Duc-Bol), Saar-Lorraine (Duc-Bol), Donets (Duc-Bol), NW Spain (Duc).

***Paripteris schuetzei* (Potonié) Daber**

- * 1903 *Neuropteris schuetzei* Potonié: 399.
- T 1912 *Neuropteris schuetzei* Potonié: 122; fig. 84.
- * 1963b *Paripteris schuetzei* (Potonié) Daber: 1212, fig. 2.

REASON FOR GENERIC ASSIGNMENT. Frond architecture and general aspect of pinnules.

OCCURRENCE. S. Limburg (Lan), U. Silesia (Duc).

Form-genus **SPHENONEUROPTERIS** Shchegolev

***Sphenoneuropteris brongniartii* Shchegolev**

- * 1979 *Sphenoneuropteris brongniartii* Shchegolev: 159; pl. 53, fig. 2.

REASON FOR GENERIC ASSIGNMENT. General similarity in pinnule morphology and venation with type species.

COMMENTS. The distinction between this and *S. elegans* is far from clear, and there must be a strong likelihood that they are synonyms.

OCCURRENCE. N. Caucasus (StC).

***Sphenoneuropteris dimorpha* (Lesquereux) Cleal & Shute, comb. nov.**

- T 1879 *Pseudopteropteris dimorpha* Lesquereux: pl. 35, figs 1–6.
- * 1880 *Pseudopteropteris dimorpha* Lesquereux: 201.
- 1978 *Neuropteris dimorpha* (Lesquereux) Boersma: 59; pl. 8, fig. 3, pl. 12, figs 1–6.

REASON FOR GENERIC ASSIGNMENT. Mainly the venation (widely forking veins, oblique to pinnule margin, producing low vein density), and the large, lax-limbed pinnules.

COMMENTS. Little is known of the frond architecture and nothing of the epidermal structure of this species. However, the pinnules show a remarkable similarity, especially in their venation (e.g. Doubinger & Germer 1975b, pl. 4), to the types of *Sphenoneuropteris*.

This species is often thought to have characteristically deeply-lobed pinnules (e.g. Wagner 1958). However, Boersma (1978) showed that this was at least partially a consequence of the thin limb of the pinnules, which rarely lay flat in the matrix, and would undulate in and out of the plane along which the fossil was split. It is unlikely that this can

explain all specimens with undulate margins, but the remnant examples may simply be from the distal regions of pinnae, where pinnules are in transition to ultimate pinnae.

This species was initially assigned to *Pseudopteropteris* Lesquereux, 1880. However, this form-genus was not typified and included within it was a variety of disparate types of frond; it is thus a *nomen dubium*, and cannot be used as an alternative name for *Sphenoneuropteris*.

OCCURRENCE. Saar-Lorraine (Bol-StB).

***Sphenoneuropteris elegans* Shchegolev**

- * 1979 *Sphenoneuropteris elegans* Shchegolev: 158; pl. 54, figs 1, 2.

REASON FOR GENERIC ASSIGNMENT. Type species.

OCCURRENCE. N. Caucasus (StC).

***Sphenoneuropteris nemejciana* (Purkyňová) Cleal & Shute, comb. nov.**

- * 1971 *Neuropteris nemejciana* Purkyňová: 168; pls 10–11.
- 1971 *Neuropteris venceslai* Purkyňová: 171; pl. 12.

REASON FOR GENERIC ASSIGNMENT. Similarity of pinnule form and venation to *S. dimorpha*.

COMMENTS. Purkyňová's specimens occur stratigraphically lower than any of the other species included in *Sphenoneuropteris*. However, it has many of the characteristic gross morphological features of that form-genus, including large pinnules (30–35 mm long) with a lax limb and somewhat undulate margin, and a low vein density (16 veins per cm on pinnule margin).

The type and only known specimen of *N. venceslai* originated from the same locality and horizon as the types of *S. nemejciana*. It has similarly large, relatively thin-limbed pinnules, thin midvein, and low vein density; compare for instance the specimen figured by Purkyňová on her pl. 11, fig. 2. The pinnules have a more acute apex, and are marginally larger, but not excessively so; the largest recorded pinnule of *S. nemejciana* is 5.5 cm long, as opposed to 7.5 cm in *N. venceslai*. All in all, there seems little reason to regard these as separate species.

OCCURRENCE. U. Silesia (Lan).

***Sphenoneuropteris praedentata* (Gothan) Cleal & Shute, comb. nov.**

- * 1909 *Neuropteris praedentata* Gothan: figs 1, 2.

REASON FOR GENERIC ASSIGNMENT. Based mainly on venation (widely forking veins, oblique to pinnule margin, producing low vein density), and the relatively large, subtriangular pinnules.

COMMENTS. The general aspect of the pinnules, particularly the venation, seems to exclude this from *Neuropteris* as it is interpreted in this work. The venation seems to fit in far better with that given in the diagnosis of *Sphenoneuropteris* given by Shchegolev (1979). It is recognized that this is far from a satisfactory basis for recognizing 'natural' form-genera. However, until cuticle and frond architecture data become available, Shchegolev's form-genus provides a convenient repository for this species.

The only large specimens of this species to have been published are in Zeiller (1888a: pl. 26) and Zeiller (1906: pl. 26), both under the name *Neuropteris crenulata* Brongniart. They both show bipinnate frond fragments, with intercalated pinnules on the penultimate rachis. Laveine (1967: text-fig. 6d) interprets the 1906 specimen as essentially a pinnate frond. However, the penultimate rachis in the 1888 specimen is noticeably curved, suggesting that it might be from a bipartite frond, similar to that present in many of the other neuropteroid form-genera.

The numerous records of this species from the Iberian Peninsula have been analysed by Knight (1983). He has concluded that, although they show some similarity to *S. praedentata*, they differ in having smaller, thinner-limbed pinnules with weaker crenulations on the margin, and thinner veins. They have since been transferred to a separate species, *S. wagneri* (see below). Significantly, Knight also observed that the Spanish material shared some features in common with *S. dimorpha*, providing some support for the idea that *S. dimorpha*, *S. praedentata* and *S. wagneri* cluster together to form a reasonably natural form-genus.

OCCURRENCE. (?)Saar-Lorraine (Bar), Massif Central (Bar-StC).

Sphenoneuropteris wagneri (Lorenzo) Cleal & Shute, comb. nov.

* 1980 *Mixoneura wagneri* Lorenzo: 11–13; pl. 1.

REASON FOR GENERIC ASSIGNMENT. The large, relatively lax pinnules with a wide venation.

COMMENTS. This species was established for the Spanish specimens that were traditionally assigned to '*Neuropteris*' *praedentata* (see comments on previous species).

OCCURRENCE. NW Spain (Bar-Aut).

Species of uncertain taxonomic position

Included here are those species which, although clearly circumscribed and thus 'good', cannot be readily assigned to any of the above form-genera. Cuticular evidence is lacking, and their pinnule and pinna morphologies do not provide any obvious comparison with one or other of the more completely known species.

Neuropteris bourozii Laveine

* 1967 *Neuropteris bourozii* Laveine: 152; pls 23–25.

COMMENTS. Some of the pinnules of this species show similarities to *Laveineopteris* (Laveine 1967: pl.24, fig.5), while others are of a more typical neuropterid-type (Ibid. pl.23, fig.5). Laveine (1967) assigned specimens from the Pennines Basin figured by Bolton (1926: pl. 6) to this species, but they almost certainly belong to *L. tenuifolia*.

OCCURRENCE. Franco-Belgian Basin (Duc), NW Germany (Duc).

Neuropteris cordata Brongniart

* 1831 *Neuropteris cordata* Brongniart: 229; pl. 64.
 . 1890 *Neuropteris Raymondii* Zeiller: 147; pl. 9a, fig. 4.

. 1893 *Neuropteris pseudoblissii* Potonié: 137.
 . 1964 *Mixoneura raymondii* (Zeiller) Wagner: 9.

COMMENTS. This species cannot readily be fitted into any of the other form-genera. The general aspect of the pinnules suggests affinities with *Neurocallipteris* or possibly even *Neuropteris*, but what little is known of the frond architecture (e.g. Langiaux 1984: fig. 111) would seem to separate it from both genera. The species is in clear need of a revision.

The type and only known specimen of *N. raymondii* Zeiller (*Mixoneura raymondii* (Zeiller) Wagner) was figured photographically by Doubinger (1956: pl. 12, fig. 3; pl. 13, fig. 1). It originated from the Mont Pel Formation in the Autun-Epinac Basin, and occurs together with specimens of *N. cordata*. The pinnules are rather smaller (c.16 mm long) than is typical for *N. cordata* but the venation is very similar. Doubinger (1956) claims that the veining density is higher in *N. raymondii*, but the measured value of 22 veins per cm on the pinnule margin is quite compatible with some of the smaller forms of *N. cordata* (cf. Zeiller 1906: pl. 27, fig. 3). In view of the evidence of association and of the similarity of the venation, it seems reasonable to assume that *N. raymondii* is merely a small-pinnuled form of *N. cordata*, possibly from the more distal regions of the frond.

N. pseudoblissii is still being recorded in the modern literature for specimens from the upper Stephanian with very elongate pinnules, but which are otherwise very close to *N. cordata*. Zeiller (1888a), who figured the types of Potonié's species under the incorrect name *Neuropteris blissii*, noted that isolated fragments would be difficult to distinguish, and it is also significant that the two species almost invariably occur together (e.g. see records in Doubinger 1956). There thus seems little justification for separating the two species.

The single specimen from the Duckmantian of the Pennines figured by Crookall (1959: pl. 41, fig. 5) as *N. pseudoblissii* is an indeterminable fragment, possibly of a mariopterid.

OCCURRENCE. Massif Central (StB-StC), Pyrenees (StC), Alps (StC), N. Portugal (StC).

Neuropteris duprei Laveine

* 1967 *Neuropteris duprei* Laveine: 164; pl.29, figs 1–4.

COMMENTS. This is a very distinctive species with elongate, often asymmetrical pinnules and very oblique lateral veins. The only other similar material reported from Europe are the specimens described by Němejč (1949, pl.1, figs 1–8) as *Odontopteris stradonicensis* Andrä. There is also a record from the Langsettian of NW Spain (Wagner & Bowman 1983), but it is not illustrated.

OCCURRENCE. Franco-Belgian Basin (Lan-Duc).

Neuropteris dussartii Laveine

* 1967 *Neuropteris dussartii* Laveine: 191; pl.48.

COMMENTS. Laveine argued that this species shared a number of features in common with laveineopterid species such as *L. loshii* and *L. rarinervis*. However, Laveine also pointed out certain similarities with *Neuropteris ovata*, such as the presence of a basiscopic auricle on some of the pinnules.

OCCURRENCE. South-West UK (Bol-WeD), Franco-Belgian Basin (WeD), NW Germany (WeD).

Neuropteris teberdensis Shchegolev

- * 1979 *Neuropteris teberdensis* Shchegolev: 163; pl. 51; pl. 52, fig. 1; pl. 53, fig. 1.

COMMENTS. The pinnules of this very late species show a marked resemblance to *Neuropteris ovata*, suggesting that it is a true neuropterid. However, one of the specimens (Shchegolev 1979: pl. 52, fig. 1) suggests that the frond might have been only bipinnately divided, with intercalated pinnules on the primary rachis branches. This fact, together with its high stratigraphical position, suggests that the species may instead belong to *Neurodontopteris*.

OCCURRENCE. N. Caucasus (StC).

Neuropteris zeilleri de Lima

- T 1864 *Neuropteris cordata* Brongniart; Göppert: 100; pl. 11, figs 1–2.
 * 1890 *Neuropteris zeilleri* de Lima: 140.

COMMENTS. This species has been widely quoted in the literature as occurring in the upper Stephanian of Europe (e.g. Havlena 1953, Doubinger 1956, Wagner 1963, Vetter 1968, Wagner & Sousa 1983). As pointed out by Zeiller (1906) and Vetter (1968), however, there are problems with the typification of the species; that quoted above is the one normally accepted, but it is far from clear if de Lima regarded Göppert's specimens or his own Portuguese specimens as types. The distinction from *Neuropteris cordata* is also far from clear and according to Zeiller is based mainly on the fact that there is not a single midvein, but a number of separate, fine veins lying along the long axis of the pinnules. This distinction has never been properly documented and there must be a strong suspicion that it is purely taphonomic. Whatever the outcome, however, there can be little doubt that *N. zeilleri* will end up in the same form-genus as *N. cordata*, whatever that will prove to be (see above).

OCCURRENCE. (?) Intra-Sudetic Basin (Aut), Massif Central (StB, StC-Aut), NW Spain (StB, ?StC), N. Portugal (StC-Aut).

Nomina dubia

The first group of species included here were initially described on just one or two fragments and additional material has not been published. There is thus insufficient evidence of morphological variation to be able to recognize the species reliably, or of features such as frond architecture or epidermal structure, by which their generic position could be ascertained. They are listed below without further comment.

Neuropteris flabellinervis Gothan, 1953: 59; pl. 9, figs 2–3; pl. 28, fig. 2; pl. 30, fig. 6.

Neuropteris asturiana Jongmans MS ex Wagner, 1962: 757 [nomen nudum].

Neuropteris beveridgei Crookall, 1959: 189, pl. 40, fig. 4.

Neuropteris bulupalغانensis Zalesky in Zalesky & Chirkova, 1933: 9; fig. 1.

Neuropteris(?) delasii Zeiller, 1892: 45; pl. 8, fig. 6.

Neuropteris dispar Zeiller, 1888a: 253; pl. 29, fig. 6.

Neuropteris horrida Zeiller, 1888a: 251; pl. 32, figs 1–2.

Neuropteris jugosa Kidston ex Crookall, 1959: 164; pl. 41, fig. 3.

Neuropteris matheronii Zeiller, 1888a: 245; pl. 28, fig. 7.

Neuropteris pseudoimpar Stockmans & Willière, 1953: 235; pl. 44, fig. 2; pl. 50, fig. 12.

Neuropteris squarrosaeformis Kidston ex Crookall, 1959: 163; pl. 50, fig. 6.

Neuropteris subsessilis Stockmans & Willière, 1955: 14; pl. 8, fig. 1.

Neuropteris waltonii Stockmans & Willière, 1953: 227–228.

In addition to the above, there are a number of other species, for which more specimens are known, but which are still impossible at present to identify reliably. These require further comment.

Mixoneura muensterifolia Němejč

- * 1949 *Mixoneura muensterifolia* Němejč: 15–16; pl. 3, figs 10–14.
 . 1949 *Mixoneura grandifolia* Němejč: 18–20; text fig. 4.

COMMENTS. Němejč established this species for a number of fragments from the middle Westphalian, that were claimed to have a pinnule shape similar to *Neuropteris obliqua*, but with more flexuous veins. These are similar to the characters used to define *N. semireticulata*, of which it would be an earlier synonym. However, the illustrations used by Němejč are poor and the specimens fragmentary. It would thus be unwise to give it priority over *N. semireticulata*, at least until Němejč's species is better documented.

Němejč reported larger pinnules in close association with *M. muensterifolia*, and used them as the types of another new species, *M. grandifolia*. However, the figured specimens would seem to correspond with forma *impar*-type pinnules found in the proximal parts of the fronds of the *N. obliqua* group. It is thus almost certain that they are conspecific with the specimens that he assigned to *M. muensterifolia*.

Neuropteris arberi Crookall

- * 1959 *Neuropteris arberi* Crookall: 148; pl. 50, fig. 7; pl. 51, figs 2–4.

COMMENTS. Based on three fragments, none of which show details of the apical pinnules or the pattern of lobing. Their affinities may be more mariopterid than neuropterid. Remy & Remy (1975) attempted to use this species for German specimens, but it is difficult to see how this can be justified in the light of the extremely imperfect types.

Neuropteris kosmannii Potonié

- * 1903 *Neuropteris kosmanni* Potonié: 399.
 T 1913 *Neuropteris kosmanni* Potonié; Gothan: pl. 47, fig. 3; pl. 50, figs 1–4.

COMMENTS. Although this species periodically re-appears in the literature (e.g. Kotasowa 1968), it has only ever been described from small fragments. They all show vaulted, extremely thick-limbed pinnules, often with a somewhat undulate margin, quite atypical for any of the neuropteroid form-genera, with the possible exception of *Margariopteris*. In the absence of more complete material, it is impossible either to give it a useful circumscription as a species, or to determine their generic position.

Neuropteris lubnensis Havlena

* 1953 *Neuropteris lubnensis* Havlena: 153–154; pl. 6, figs 1–2.

COMMENTS. This is based on forty-eight specimens preserved in a sandstone, although only two were figured. They are undoubtedly unusual, having very large pinnules (up to 4 cm long and 2 cm wide), and do not fit into any previously described species. However, the arenaceous matrix is far from perfect for preserving this type of fossil, and the number of specimens illustrated is inadequate to determine the range of morphological variation, let alone frond architecture. Much better material needs to be documented before anything can be done with this species.

Neuropteris montana Heer

* 1879 *Neuropteris montana* Heer: 22; pl. 6, figs 22, 23.

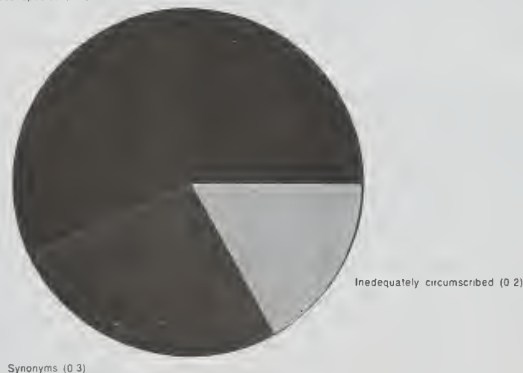
T 1960 *Neuropteris montana* Heer; Jongmans: pl. 21, fig. 121.

COMMENTS. From the form of the distal part of the pinna, the type clearly belongs to a paripinnate frond, presumably of the Potonieaceae. It is reputed to originate from the Cantabrian or lower Barruelian, which is far higher stratigraphically than *Paripteris* normally occurs. The venation is very poorly preserved, but may be anastomosed with very elongate vein-meshes. If so, then it may belong to *Linopteris neuropteroides* (Gutbier) Potonié, 1899, which sometimes occurs as high as Barruelian. However, the material is really inadequate to give an unequivocal statement on this.

ROBUSTNESS OF GENERIC TAXONOMY

The statistics of this taxonomic analysis are summarized in Table 2 and Fig. 18. A total of 101 neuropteroid species have been recorded from Europe over the last half century, of which nearly a half (43.5%) are either unsatisfactory because they are based on insufficient material, or are later synonyms of other species. Of the remaining fifty-seven 'good' species, all but six (10.5%) can be assigned to one or other of the 9 form-genera summarized in the early part of this paper.

Total good species (0.6)



DIVERSITY ANALYSIS

Diversity of the neuropteroids as a whole

As a by-product of this study, whose original goal was merely to ascertain the robustness of the generic classification of neuropteroid fronds, we have built up a database of the stratigraphical and geographical distribution of species within Europe. This would appear to invite further analysis of diversity variations. Diversity analysis has become a popular pursuit in recent years, but can be prone to serious problems

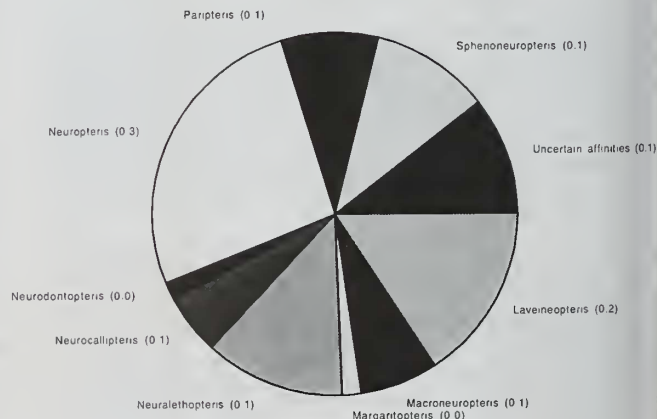


Fig. 18 The robustness of the taxonomy of neuropteroid fronds. (a) The proportions of synonyms, inadequately described and 'good' species among all those neuropteroids used since 1940. (b) The proportion of the 'good' species belonging to each of the form-genera.

The six species that cannot yet be placed in our generic classification fall into three groups.

1. *N. cordata* and *N. zeilleri* appear closely related to each other and it is far from certain that they are not in fact conspecific. Although widely recorded from the Stephanian and Autunian of France and the Iberian Peninsula, little is known of the frond architecture and nothing of the cuticles (the cuticles assigned to *N. cordata* by Barthel, 1976, in fact belong to *Neurodopteris auriculata* – see above).

2. *N. duprei* has unusual, asymmetrical pinnules unlike any of the other species included in this analysis; in fact they are different from any type of foliage previously assigned to the trigonocarpaleans. It may well belong to a new form-genus, but details of the frond architecture and/or cuticles will be needed before any decision on this can be made.

3. From the general aspect of the pinnules, it is likely that *N. bourozii*, *N. dussartii* and *N. teberdensis* belong to either *Neuropteris*, *Laveineopteris* or *Neurocallipteris*. Again, evidence of frond architecture and/or cuticles will be needed before a decision can be made on their classification.

In conclusion, the analysis has allowed us to see where the main gaps are in our knowledge of these fossil fronds. In particular, the 6 species that cannot currently be assigned need to be further investigated. Nevertheless, we believe that the results support the essential robustness of our generic classification of neuropteroid fronds, and points to it being a potentially useful tool for understanding more clearly the distribution of these plants.

Table 2 Statistics of neuropteroid taxonomy

Form-genera	No. of species	% (Total)	% (Good)
<i>Laveineopteris</i>	9	8.91%	15.79%
<i>Macroneuropteris</i>	4	3.96%	7.02%
<i>Margaritopteris</i>	1	0.99%	1.75%
<i>Neuraethopteris</i>	7	6.93%	12.28%
<i>Neurocallipteris</i>	3	2.97%	5.26%
<i>Neurodontopteris</i>	1	0.99%	1.75%
<i>Neuropteris</i>	15	14.85%	26.32%
<i>Paripteris</i>	5	4.95%	8.77%
<i>Sphenoneuropteris</i>	6	5.94%	10.53%
Uncertain affinities	6	5.94%	10.53%
Inadequately circumscribed	17	16.83%	
Synonyms	27	26.73%	
Total 'good' species	57	56.44%	
Total 'bad' species	44	43.56%	
Grand total	101	100.00%	

due at least in part to the tendency to use data trawled uncritically from the literature (cf. comments by Cleal 1988). Our database, although based only on a small range of species, at least has the merit of having been critically compiled.

To this end, a tabulated set of statistics has been compiled to represent diversity, first-appearances and extinctions for each stage (Table 3). This has been done separately for each of the form-genera, as well as for the group as a whole (including those species unassignable to any of the form-genera).

The diversity of the group as a whole follows a fairly simple pattern, showing a marked peak in the Westphalian, followed by a rapid decline and then a subsidiary peak in the upper Stephanian (Fig. 19A). The Westphalian peak would seem to be confirmed by observations made by Boulter *et al.* (1988) on diversity changes in the wider plant adpression record for the palaeoequatorial belt. It almost certainly reflects variations in the available non-marine strata in Europe; Niklas *et al.* (1980, p. 29) demonstrated that 98.5% of plant fossil diversity (at least between the Carboniferous and Jurassic) can be accounted for by this single factor. Numerical data on the available strata in each stage are not available for Europe. However, our observations would seem to confirm the general impression that delta-plain, fluvio-lacustrine deposits, which presumably reflect the habitats favoured by the plants producing these fronds, are at a maximum in the Westphalian and upper Stephanian, with a low in the Cantabrian and, to an extent, the Baruellian.

Figs 19B and 19C show the patterns of appearances and extinctions per stage, both corrected for variation in the length of the stage. These show curves with a similar double-peaked form to the diversity curve. A broad correlation between species turn-over and diversity is not surprising. However, the species profit/loss curve (Fig. 19D) shows a more interesting pattern. Up to the Kinderscoutian the situation is relatively stable, but at higher stratigraphical levels there are major fluctuations. Peaks occur in the Kinderscoutian, Langsettian and Baruellian/Stephanian B. The first of these can be correlated with the first appearance of large-scale deltas across northern Europe; the second the

proliferation of coal-swamp conditions on the delta-tops; and the third the expansion of intra-montane basins in central and southern Europe. The trough in the Cantabrian presumably reflects the change-over from predominantly paralic to predominantly intra-montane conditions over much of Europe.

So, the diversity of the neuropteroids as a whole is merely a function of the general diversity of the tropical swamp vegetation. If the form-genera outlined earlier in this paper have any basis in the genetic relationships of the parent plants, diversity patterns of the individual form-genera may tell a different story. Fig. 20 shows the diversity curves of six of the most abundant of the form-genera plotted separately. This clearly shows that the story is far more complex. However, the style of analysis dealt with so far in this paper is not really suitable for uncovering the more detailed distributional patterns. For this, we need to look at the detailed variations in diversity of the species within each of the form-genera.

The problem here is the limited amount of suitable data available. There have been studies documenting the quantitative stratigraphical variations of different species, such as by Davies (1929). However, such work is mostly old, largely unillustrated and uses unreliable taxonomy. Also, as pointed out by Scott (1985), there are serious weaknesses with the sampling that was usually employed. Scott himself suggested that quadrat analysis, similar to that sometimes used to study living plant ecology, could produce more reliable results. However, while quadrat analysis might prove valuable in the detailed relationship between facies and plant fossils at a specific locality, it would need a considerable number of such studies before it would reveal any meaningful stratigraphical patterns of plant fossil distribution.

We have instead adopted an alternative approach, by looking at the numbers of localities from where a species is recorded at different stratigraphical levels. To do this, it was decided to restrict the analysis to one particular area, which would help minimize potential palaeolatitudinal variations. The area should have numerous records spread over a reasonably long stratigraphical range. The data should also preferably be based on identifications made by a single authoritative palaeobotanist, thus minimizing the potential for subjective variations in identification. In fact, only one area was found to have all these virtues, namely the Franco-Belgian Basin, through the monographic study by Laveine (1967).

Species diversity analysis (Franco-Belgian Basin)

Laveine's (1967) monograph provides a taxonomically reliable record of most of the neuropteroid species found in the paralic belt between the Kinderscoutian and Westphalian D. For each species, he individually lists the localities where they are found in the Nord-Pas-de-Calais Coalfield, divided stratigraphically into lower, middle and upper divisions of the formations there. Using this data, we have plotted the diversity curves for each species of four of the form-genera (Figs 21–23).

Neuropteris (Fig. 21). These 7 species appear to fall into two groups. The early group consists of *N. obliqua*, *N. heterophylla*, *N. ghayei* and *N. willieri*, which occur predominantly in the Langsettian and basal Duckmantian (in Belgium, *N. obliqua* is reported to extend down to the Marsdenian, but the French records on which the present

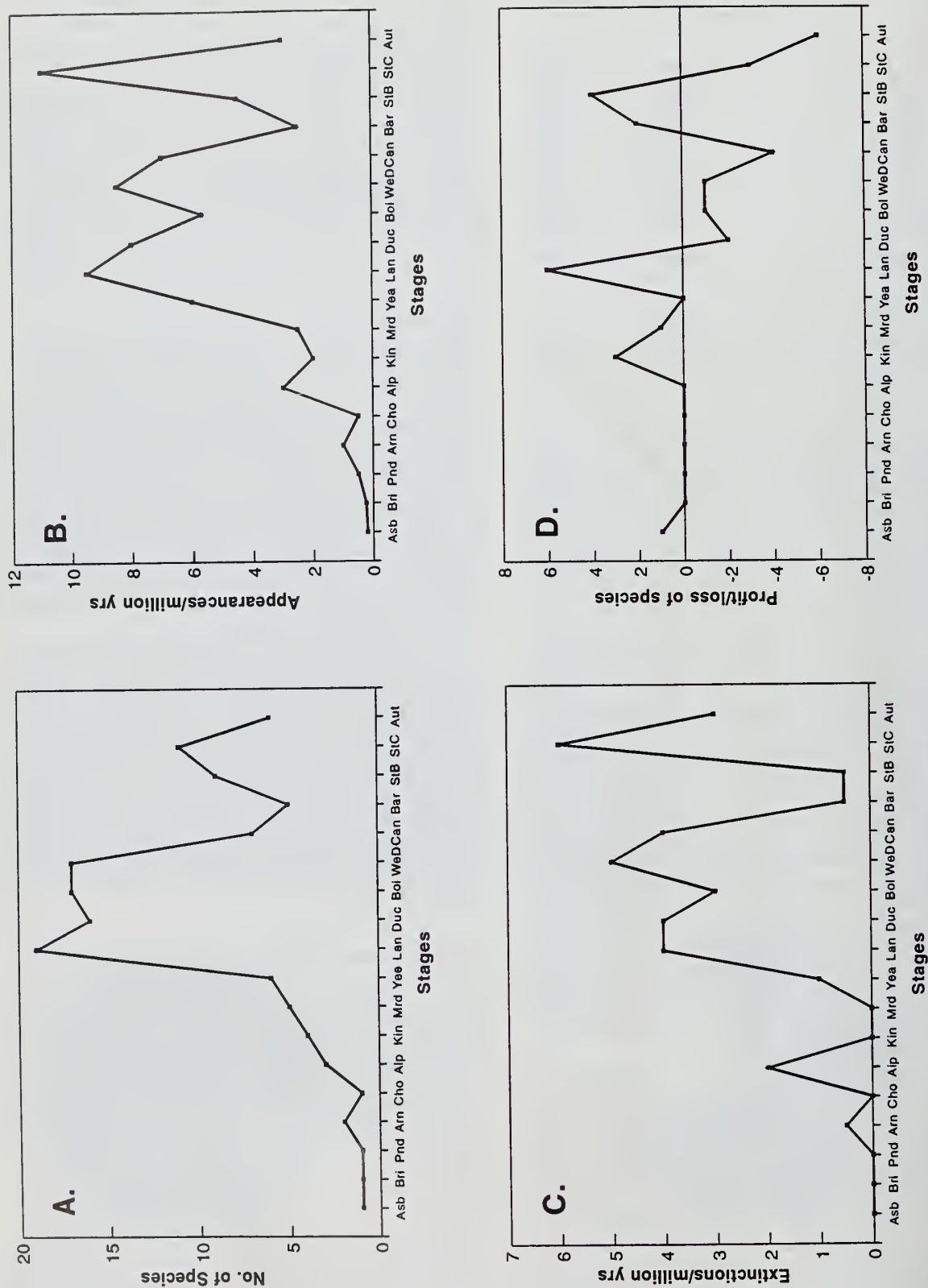


Fig. 19 Diversity curves for the group of neuropteroid species as a whole: (a) number of species appearing per million years in each stage; (b) number of species appearing per million years in each stage; (c) number of species extinctions per million years in each stage; (d) profit/loss of species in each stage.

Table 3 Diversity variations in Neuropteroid genera.

Stage	Laveineopteris			Macroneuropteris			Neuradelethopteris			Neurocallipteris			Neuropteris			Paripteris			Sphenoneuropteris			Total		
	N	F	TF	L	N	F	TF	L	N	F	TF	L	N	F	TF	L	N	F	TF	L	N	F	TF	L
Asb													1	1	13.0						1	1	13.0	
Bri													1								1			
Pnd													1								1			
Arm													1								1			
Cho								1	1	10.0											2	1	5.0	1
Alp								1													1			
Kin								3	2	5.0			1	1	0.5	1					1			
Mrd								3													1			
Yca								3					1	1	10.0		1	1	8.0		3	2	0.5	2
Lan	3	3	4.3					6	4	0.8			2	1	5.0		1				5	1	2.0	
Duc	5	2	0.6	2									4	2	1.5	1	2	1	3.0	1	19	14	2.4	8
Bol	5	2	3.1	3									4	2	3.5	2	4	2	5.0	2	16	6	2.3	8
WeD	3	1	0.2	2									6	3	1.5	3	3	1	2.0	3	17	8	2.4	9
Can	1			1									7	4	2.7	5				1	17	9	1.9	10
Bar													2			1				1	7			4
StB																				3	2	7.5	1	
StC													1	1	0.2	1				2	9	5	3.4	1
Aut													1			1				4	2	0.2	3	
													2							1				6

N = Number of species present in stage.

F = Number of first appearances in stage.

TF = Average duration (in million years) of species first appearing in stage.

L = Number of extinctions in stage.

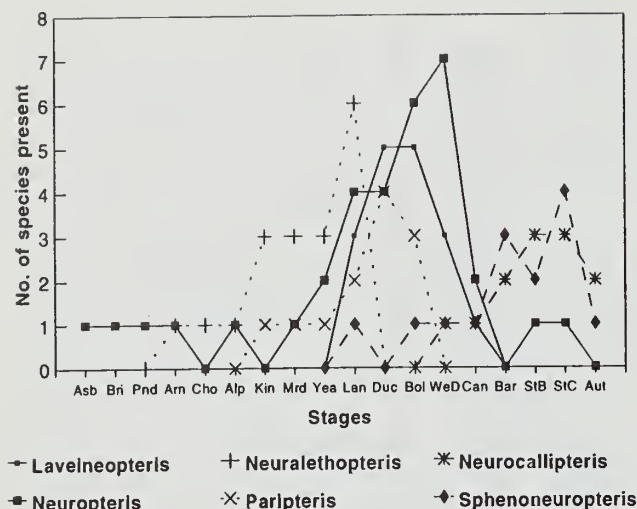


Fig. 20 Stratigraphical diversity of six of the more abundant neuropteroid form-genera, showing complexity hidden by generalized graph in Figure 19a.

analysis is based only show it as far back as the Langsetian). It then undergoes a significant decline in the lower Duckmantian. Only one of the species extends much beyond the middle Duckmantian, and that is what is referred to in the chart as the *N. obliqua* group. This pattern seems to be in general agreement with what is seen in areas other than the Franco-Belgian Basin.

As with the other neuropterids, *N. obliqua sensu stricto* undergoes a marked decline in the lower Duckmantian. However, in the upper Duckmantian there is the start of a progressive change in the venation, which becomes more flexuous and eventually culminates in the anastomosed-veined form known as *Reticulopteris* Gothan. Details of this gradual change in venation through the Duckmantian and Bolsovian have been documented by Josten (1962), and the possible adaptive advantage of this style of venation is discussed by Zodrow & Cleal (1993). This morphological change is accompanied by a proliferation of the group of species, especially in the Bolsovian.

The abundance of the *N. obliqua* group then undergoes a dramatic collapse in the topmost Bolsovian and it eventually becomes extinct in the upper Westphalian D. This collapse in abundance coincides approximately with the appearance of the second group of neuropterids at the base of the Westphalian D. In the Franco-Belgian Basin, this consists of just one species, namely *N. ovata*, but elsewhere in Europe there are other, very similar species which come in at about the same level (*N. flexuosa*, *N. plicata* and *N. ervedosensis*). This is near the top of the Upper Carboniferous succession in this basin and so provides no direct evidence of the diversity of these neuropterids at higher levels. However, in other areas such as South Wales (Cleal 1978) and NW Spain (Wagner *et al.* 1983, Wagner & Alvarez-Vázquez 1991) it is clear that the group continues to be abundant at least through the Westphalian D and Cantabrian, and in some cases beyond.

There is no direct evidence from the Franco-Belgian Basin of the phylogenetic origins of the *N. ovata* group. There is a possible precursor in the Bolsovian of the Intra-Sudetic Basin (*N. praeovata*), but this throws little light on potential ances-

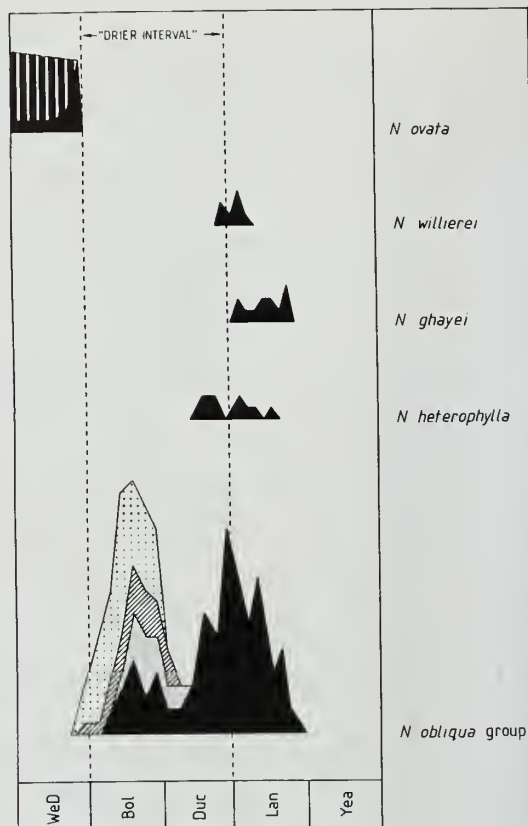


Fig. 21 Detailed abundance variations of *Neuropteris* species, plotted against stages (using abbreviations shown in Fig. 2). In the graph of the *Neuropteris obliqua* group, black represents *N. obliqua*, fine stippling *N. parvifolia*, diagonal hatching *N. semireticulata*, and coarse stippling *Reticulopteris muensteri*. Based on data from Laveine (1967), determined from the Franco-Belgian Basin. The shaded expansion of the *N. ovata* curve reflects its proliferation in other areas.

tors. Almost certainly, the group evolved in an extra-basinal habitat, possibly from a *N. heterophylla*-like ancestor.

Laveineopteris (Fig. 22). The laveineopterids may be divided into two main groups: those with larger pinnules (the *L. tenuifolia/loshii* group) and those with smaller pinnules (the *L. rarinervis* group). The larger pinnuled-group first appears in the Langsetian with *L. loshii*, which reaches its acme in the upper Langsetian. At about the Langsetian-Duckmantian boundary, however, it undergoes a significant decline in abundance, and is replaced by a number of species with more elongate pinnules (*L. tenuifolia*, *L. hollandica*, *L. jongmansii*, *L. morinii*). These species, especially *L. tenuifolia*, remain abundant and characteristic elements of the Duckmantian and Bolsovian, but then towards the top of the Bolsovian decline sharply to become extinct in the lower Westphalian D.

The *L. tenuifolia* group shows a reduction in abundance at about the Duckmantian-Bolsovian boundary, but is otherwise an important and characteristic element found in those stages. However, towards the top of the Bolsovian it undergoes a second and this time terminal decline, finally becoming extinct in the basal Westphalian D.

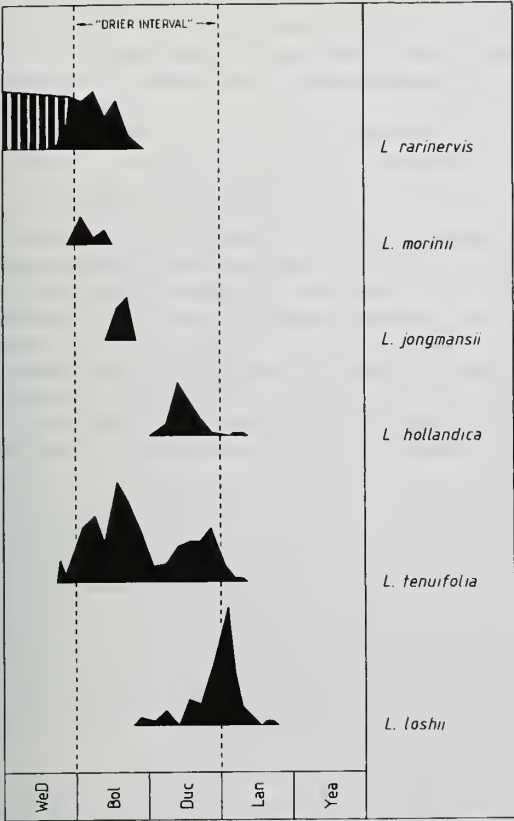


Fig. 22 Detailed abundance variations of *Laveineopteris* species, plotted against stages (using abbreviations shown in Fig. 2). Based on data from Laveine (1967), determined from the Franco-Belgian Basin. The shaded expansion of the *L. rarinervis* curve reflects its proliferation in other areas.

The *L. rarinervis* group of very small-pinnuled species shows a somewhat different distributional pattern. In the Franco-Belgian Basin it starts in the Bolsovian, having possibly originated from the slightly older *L. nicolausiana*. It proliferates during the Bolsovian. In the lower Westphalian D it appears to decline in the Franco-Belgian Basin, but this is symptomatic of it being at the top of the Upper Carboniferous succession here; elsewhere in the paralic belt of the Cantabrian, it continues to be abundant through into the Cantabrian.

Neuraethopteris (Fig. 23). It is well known that this form-genus is restricted to the Namurian and Langsetian, a point which is borne out by the Franco-Belgian data. The only other point of possible significance is that, compared with many of the other neuropteroid taxa whose extinctions are normally marked by a gradual decline in abundance, the extinctions of most of the neuraethopterids is characterized by a sudden proliferation followed by a sudden decline.

Paripteris (Fig. 23). According to Laveine *et al.* (1989), the plant that bore paripterid fronds migrated from China to Europe in the early Namurian. Elsewhere in Europe, it first appears in the Kinderscoutian, while in the Franco-Belgian Basin its lowest occurrence seems to be in the Marsdenian. The stratigraphically lowest species is *P. gigantea*, which

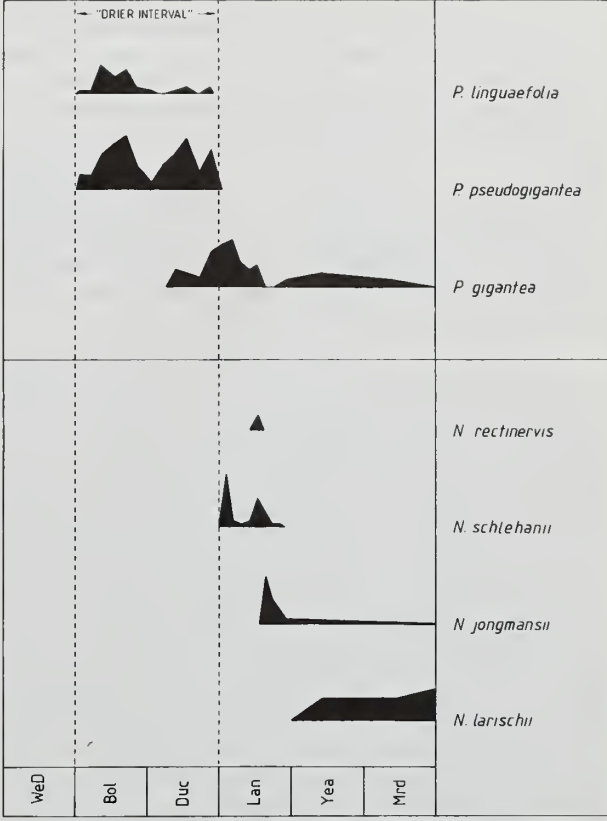


Fig. 23 Detailed abundance variations of *Neuraethopteris* and *Paripteris* species, plotted against stages (using abbreviations shown in Fig. 2). Based on data from Laveine (1967), determined from the Franco-Belgian Basin.

extends through the rest of the Namurian, and proliferates in the Langsetian.

At about the start of the Duckmantian, *P. gigantea* starts to show a progressive decline, and is replaced by a new set of species (*P. pseudogigantea*, *P. linguaeifolia*). These remained important elements of the Duckmantian and Bolsovian equatorial floras, except for a brief and temporary decline near the Duckmantian-Bolsovian boundary. Towards the top of the Bolsovian, however, these paripterids start a more significant reduction in abundance, and they eventually become extinct just below the base of the Westphalian D.

Macroneuropteris. Only one species of this form-genus occurs in the Franco-Belgian Basin (*M. scheuchzeri*), and so it has not been shown on the charts. The lowest occurrence of *M. scheuchzeri* here is in the upper Duckmantian, although elsewhere it has been documented from as low as the upper Langsetian (Pennines Basin – Cleal 1979). It reaches an acme in the upper Bolsovian and then appears to decline. However, it should be noted that elsewhere it remains an abundant species through to the Cantabrian.

Palaeoecological controls on species distributions

From the above analysis of species distributions, a clear pattern has emerged. Most significantly, there are two major stratigraphical levels where changes occur:

1. The Langsettian-Duckmantian boundary. This marks (a) the extinction of *Neuraethopteris*, (b) the start of the decline of the early group of *Neuropteris* species, (c) the transition from *Laveineopteris loshii* to the more elongate-pinnuled laveineopterids (*L. tenuifolia* group), and (d) the transition from *Paripteris gigantea* to *P. pseudogigantea* and *P. linguafolia*.

2. The Bolsovian – Westphalian D boundary. This marks (a) the extinction of *Paripteris*, (b) the decline and eventual extinction of *Laveineopteris*, (c) the decline and eventual extinction of *Reticulopteris* and *Neuropteris semireticulata*, and (d) the sudden appearance and proliferation of the second group of *Neuropteris* species allied to *N. ovata*.

It is clearly tempting to search for a palaeoecological explanation for these two 'events', and we believe that such an explanation can be found in the results of the coal ball analyses summarized by DiMichele *et al.* (1985). Their model was based on a number of different lines of evidence from the peat-accumulating habitat vegetation, including species composition and the extent of the peat deposits. It seemed to show that through the Late Carboniferous edaphic conditions in the swamps would vary, with some periods of time being slightly drier than others. In the middle Westphalian, for instance, they found that some of the arborescent lycophyte genera declined (e.g. *Lepidophloios*, *Diaphorodendron*) and there was a corresponding increase in the *Mesoxylon*/*Mitrospermum*-type cordaites, which they interpreted as indicating rather drier conditions. From the point of view of our study this is significant, as this drier interval ranged from about the start of the Duckmantian to the end of the Bolsovian, which exactly fits with the neuropteroid distributional patterns that we have found. To make this clear, we have plotted this 'drier interval' on the distributional charts in Figs 21–23.

If the correlation between the coal ball data and the neuropteroid distributions can be accepted, it has a number of significant results:

1. *Neuropteris* species, except for those that developed a significantly flexuous to pseudoanastomosed venation, were mainly restricted to the wetter interval.

2. The development of flexuous, pseudoanastomosed and eventually reticulate veining in *Neuropteris*/*Reticulopteris* occurred when there was a change to drier conditions. It would seem to have been caused by a fundamental change of the genotype as, when conditions reverted to being wetter in the Westphalian D, *Reticulopteris* was unable to reverse the change.

3. The earliest known laveineopterid (*L. loshii*) was commonest at the time of wetter conditions in the Langsettian. This was replaced as the dominant member of the form-genus by the more elongate pinnuled forms (*L. tenuifolia*, *L. jongmansii*, *L. hollandica*, *L. morinii*) when conditions became drier, at about the Langsettian-Duckmantian boundary. The change was gradual and some pockets of *L. loshii* persisted through to the early Bolsovian (for instance, the well-known Duckmantian flora of the Barnsley Seam of Yorkshire, U.K.).

4. The reversion to wetter conditions in the Westphalian D coincided with the rapid decline and eventual extinction of the elongate pinnule forms of laveineopterid.

5. The small pinnule forms of *Laveineopteris* (*L. rarinervis*) appear not to be constrained by the same environmental factors as the rest of the species. They first appeared in the

drier interval of the middle Westphalian, but seemed equally at home in the wetter conditions of the Westphalian D. *Macroneuropteris* would seem to have been similarly unaffected by the environmental change in the early Westphalian D.

6. Like the laveineopterids, there was just one paripterid species in the first wet interval (*P. gigantea*). It appears to have many features in common (although it is not exactly the same species – Laveine, pers. comm., 1992) with the paripterids found in the upper Viséan of China, which are thought to represent the ancestral stock of this form-genus (Laveine *et al.* 1989, 1992). According to the Laveine *et al.* model, paripterids spread out westwards from China during the very late Viséan and early Namurian, along the northern coast of the Proto-Tethys Ocean. It is likely that these early paripterids favoured the wetter habitats of the lower delta plains. It would thus not be surprising that the earliest paripterid in Europe (*P. gigantea*) would also favour wetter habitats.

7. Again, like the laveineopterids, on the change to drier conditions in the early Duckmantian, the early species (*P. gigantea*) declined rapidly and was replaced by *P. pseudogigantea* and *P. linguafolia*. Both of these later species may have been adapted to the drier conditions of the middle Westphalian and did not survive the return of wetter conditions in the Westphalian D. This resulted in the extinction of the whole form-genus, although the group as a whole persisted through to the lower Stephanian in the form of its reticulate-veined cousin *Linopteris*.

8. The upper Duckmantian and lower Bolsovian has numerous marine bands, indicating a change to lower delta plain conditions (Guion & Fielding 1988). This coincides with a temporary decline in abundance of both the laveineopterids and paripterids, which then recovered in abundance when middle delta plain conditions returned in the middle and upper Bolsovian. The levees were almost certainly of lower topography in a lower delta plain setting, and thus represented wetter conditions than the levees of the upper Langsettian and lower Duckmantian. This seems to confirm that these mid-Westphalian laveineopterids and paripterids were more abundant in drier conditions.

9. The neuraethopterids appear to have been totally restricted to the wetter conditions prevalent in the Langsettian. Unlike the laveineopterids and paripterids, they seemed unable to adapt to the change to drier conditions in the Duckmantian and became extinct.

The correlation between these events, identifiable in the adpression record, and the changes in the coal-swamp petrifications is remarkable, but it is evident that they are not sharp events. For instance, the start of drier conditions probably ranged through the lower part of the Duckmantian, while the return of wetter conditions gradually developed from the topmost Bolsovian to the lower Westphalian D. This is suggested by the moisture curve given for coal-swamps by DiMichele *et al.* (1985, fig. 8.1), but the much better evidence that we have from the adpression record demonstrates it far more clearly.

DiMichele *et al.* (1985) argue that the 'wetter' and 'drier' conditions in their model refer to the edaphic conditions, which in turn were responses to variations in climate. However, whether these climatic changes were in the swamp forests themselves, or in the hinterlands that supplied the river-waters is not clear. That the changes can be identified

over wide geographical areas in North America and Europe suggests that climate may well have been a major factor. However, the temporary decline of the laveineopterids and paripterids in the upper Duckmantian and lower Bolsovian, suggests that the topography of the levees may also have been a controlling factor.

Species diversities in other areas

As already stated, it is impossible to do the same type of detailed diversity analysis in the other areas as we have done in the Franco-Belgian Basin. However, there are a few points which can be made on the distributions in some of these other places.

It is well known that in Saar-Lorraine, *Laveineopteris tenuifolia* becomes prematurely extinct in the upper Bolsovian (e.g. Laveine 1989). This is normally interpreted as a response to an environmental change in this basin, represented by a predominantly arenaceous interval known as the Geisheck Formation. From what we have learnt in the Franco-Belgian Basin, it is tempting to suggest that the Geisheck Formation represents rather wetter conditions to that represented in the underlying Sulzbach Formation, in which *L. tenuifolia* occurs commonly.

Macroneuropteris scheuchzeri also becomes prematurely extinct in the Geisheck Formation of the Saar-Lorraine (Laveine 1989). This might be regarded as unexpected, as macroneuropterids in the Franco-Belgian Basin seem relatively tolerant of environmental change. However, Bertrand (1930) suggested that the Saar-Lorraine representative of this form-genus might not be taxonomically identical to that seen in the paralic basins, having somewhat smaller pinnules with only one (rather than two) basal lobe. Although this view has not been widely accepted in the literature, the differences in response to environmental change may support Bertrand's original contention.

Over much of Europe, *Neuropteris sensu stricto* is rare in the Duckmantian and Bolsovian. A significant exception is in NW Spain, where *N. resobae* occurs abundantly in the Duckmantian Curavacas Formation (Cleal 1981). This still fits in with the general pattern, however, as the Curavacas Formation is a unit of fluvialite deposits in an otherwise marine succession (Martínez García *et al.* in Martínez Díaz 1983) and would thus presumably have wetter edaphic conditions than present in the coalfields of the paralic belt.

Over much of Europe, *Neuropteris sensu stricto* undergoes a significant decline in the lower Stephanian. This is in agreement with the DiMichele *et al.* (1985) model, as they claim that a second (and this time more significant) drier interval started in the Cantabrian or early Barruelian in the coal-swamp habitats. In a few parts of Europe, however, *Neuropteris* remains a significant component in the upper Stephanian, such as Gard and La Mure (two of the coalfields of the Massif Central), NW Spain, N. Caucasus, Donets and the Alps. This may indicate that these areas were environmentally wetter compared with the other parts of Europe and the paralic coalfields of North America.

In most of the other parts of Europe, *Neurocallipteris* is the dominant neuropteroid form-genus in the drier interval of the Stephanian. At least some also extend up into the Autunian, which DiMichele *et al.* (1985) claim represents a return to wetter conditions. However, it is far from clear that these basal Permian beds are indeed wetter and, at least in Europe, not supported by the increasing presence of red-beds.

Table 4 Results of regression and correlation analyses of extinction (L) rates against numbers of species present (N).

	No. of species of same form-genus	Total No. of species
Regression equation	$L=0.57N+0.22$	$L=0.13N+0.48$
Correlation coefficient (r)	0.7807	0.5402
Level of confidence that correlation is significant	99.99%	99.47%
Coefficient of determination	60.94%	29.18%

Species diversity and survival

We have so far indicated that at least some of the variation in diversity within the neuropteroid fossil record can be correlated with Palaeozoic climatic fluctuations, and with variations in the volume of suitable strata. However, it is to be expected that other factors may have had a role. One in particular, which our data is suitable to test, is the degree to which extinction rates were controlled by competition.

This has been tested by a regression and correlation analysis of the numbers of species present in each stage against the number of species of each form-genus that become extinct in that stage. Two separate analyses were performed, one using the total number of species present as the independent variable, and the other using the number of species of the particular form-genus present. In this way it was hoped to determine whether competition within a form-genus was a more important factor in determining extinctions than competition generally within the neuropteroid complex as a whole.

The results are summarized in Table 4 and Fig. 24. The first thing that is evident is that extinctions are significantly correlated with both the number of species of the same form-genus and the total number of species. However, the level of significance is much higher in the analysis using the number of species of the form-genus. Also, the coefficient of determination (the proportion of the variance in extinction rates due to variations in species numbers) is much greater; nearly two-thirds of the variance in extinctions could be accounted for by the number of species of the same form-genus present, while less than a third is accounted for by the total species numbers.

From this, we conclude that competition was an important factor controlling extinction rates of these plants, and that it was greater between species of the same form-genus than within the neuropteroid complex as a whole. The fossils represent plants that grew in a fairly narrow band of habitats and so some level of competition would be expected between most of the elements represented. However, in such a setting it would seem reasonable to expect that competition would be greatest between those species that were closest genetically. In this light, it would seem that the form-genera outlined in this paper truly reflect the genetic relationships between the parent plants, and thus support the essential robustness of the classification.

PALAEOPHYTOGEOGRAPHY

All of the records analysed in this paper originate from what

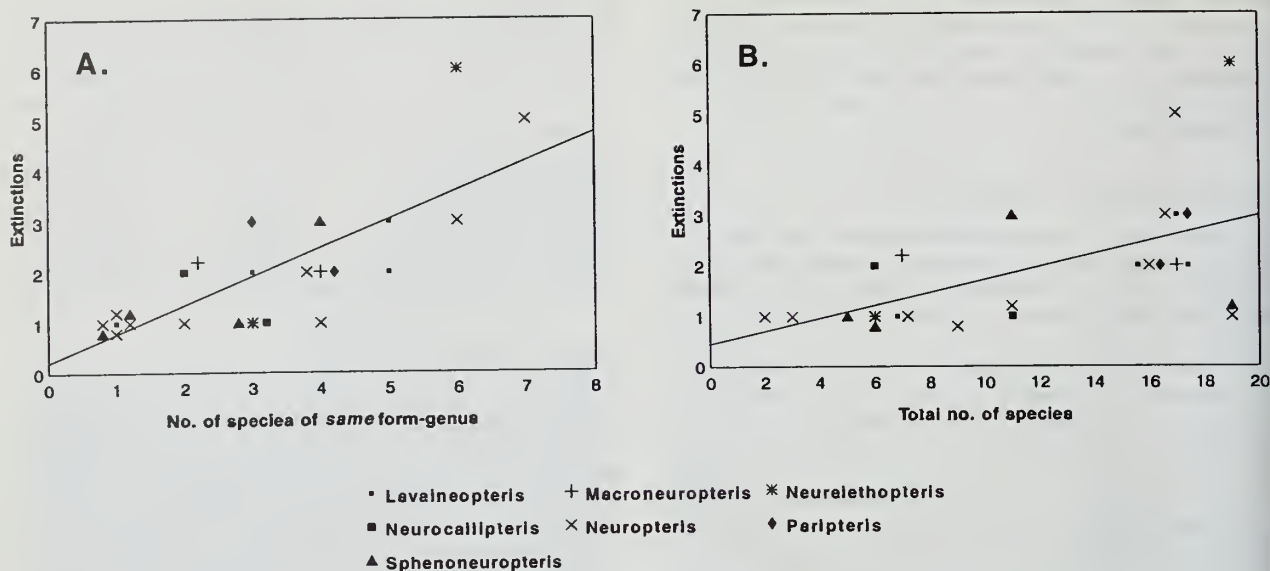


Fig. 24 Regression of extinction rates against species numbers (parameters L against N of Table 3); (a) regression against number of species of same form-genus; (b) regression against total number of neuropteroid species.

Cleal & Thomas (*in* Cleal 1991) refer to as the Europe Palaeoarea, one of the subdivisions of the Eurameria Palaeo-kingdom. There have been suggestions that this phytochorion can be further subdivided based on the plant fossil record (e.g. Gothan 1954). To investigate this possibility, we have examined our data using cluster analysis, to see if any palaeophytogeographical structure can be discerned. Our data is obviously not entirely suited to such an analysis, as it only represents a small portion of the total fossil assemblages. On the other hand, our data has the merit of having been critically assessed, and is thus preferable to some of the other recently published palaeogeographical analyses, based on uncritical literature trawls.

The database

Initially, we attempted to look at the data as a whole, using an algorithm that could account for empty data points. This was so the analysis could take into account species being sometimes absent from an area merely because there is no strata of the appropriate age there, rather than there being any fundamental phytogeographical reason. However, the results were disappointing, revealing little structure that could be related to the geographical distribution of the areas. It seemed a strong possibility that the empty data points may have significantly distorted the results.

To overcome this, the data was split into five, stratigraphically separate blocks. This reduced the number of empty data points to a much lower and acceptable level. It also allowed us to see if there was any stratigraphical variation in the geographical patterns. The starting-point was taken at the Chokierian, as there were too few neuropteroid species at lower levels to provide any meaningful results.

Chokierian – Yeadonian. This corresponds to most of the Namurian and includes records from 11 areas. *Margaritopteris multivenosa* and *Neuropteris bohdanowiczii* were removed from the original data matrix. These species are only known from the Alportian, and strata of this age are

absent in 5 out of the 11 areas. It was thought that might seriously distort the results. This left 6 species, on which the clustering was based.

Langsettian. Originally 15 areas were clustered based on 18 species. However, the records for South Limburg were omitted, in order that this analysis would be in conformity with that for the next stratigraphical interval (see below).

Duckmantian – Bolsovian. Originally 14 areas were clustered based on 24 species. The initial result showed a major discrepancy with the position of South Limburg, which appeared to cluster at a low level with Turkey, South Spain and the Alps, rather than with the other areas of the paralic belt, as would be expected. On examining the data matrix, it seemed likely that this might be due to the inadequacy of the data from South Limburg, and so we decided to omit it from the analysis (and in consequence from that of the Langsettian).

Westphalian D – Cantabrian. 15 Areas were clustered initially based on 14 species. The results were initially unsatisfactory, showing what seemed to be a strong 'chaining pattern, indicative of poor structure in the data. However, by combining the records of *Neuropteris plicata* with *N. ovata* and of *Laveineopteris piesbergensis* with *L. rarinervis*, a rather better structure became evident (the taxonomic rationale for combining these species can be found in the systematic section of this paper, although at this stage we are reluctant to make formal proposals of synonymy until the type material is subjected to a more rigorous morphological investigation).

Barruelian – Autunian. This corresponds to most of the Stephanian plus the basal Permian. The initial data set consisted of 10 localities and 14 species. However, Saxon and the Pyrenees were excluded, as they only contain record from the Autunian, and would thus distort the analysis. Also the record of *Macroneuropteris scheuchzeri* from the Inter Sudetic Basin, and of *Neuropteris schaeferi* from Saar

Lorraine were excluded. There are doubts about the reliability of the former record (see comments in systematics section) and the latter is based only on a single small fragment. The final analysis was thus run on 8 localities using 12 species.

Results

The dendrograms produced by the five analyses are shown in Fig. 25. Up to the Westphalian D, a relatively simple pattern can be seen. Many areas contain neuropteroid assemblages of relatively low diversity, in the Namurian consisting of *Neuraethopteris schlehanii* and *Paripteris gigantea*, these being supplemented by *Neuropteris obliqua* in the Langsettian. In the Duckmantian and Bolsovian, *N. schlehanii* disappears from these low diversity assemblages, and *P. gigantea* is replaced by *P. linguaeifolia*. Against this background of low diversity assemblages, however, there are two assemblage-groups that are of significantly higher-diversity and, perhaps significantly, correlate with the areas of greatest coal production. These are shaded on the dendrograms, and may be summarized as follows.

1. The Paralic Belt assemblages. These include the most diverse and abundant assemblages of neuropteroids, and consistently cluster together with Jaccard Coefficients of 45 or more from the Namurian to the Bolsovian. In the Namurian it includes most assemblages of northern, central and eastern Europe, although there is some suggestion that there is an area of even greater diversity, particularly of *neuraethopterids*, in France-Belgium, NW Germany, U. Silesia and N. Caucasus. In the Westphalian, however, the group as a whole is limited to the paralic-belt coalfields of northern Europe (NE Germany and Lublin are not included in the Langsettian, but this may merely reflect the limited data available from these areas).

2. The intra-montane basin assemblages. Assemblages from Saar-Lorraine and the Intra-Sudetic basins take on a distinctive character in the upper Duckmantian and Bolsovian. While including some taxa also found in the paralic belt assemblages, many important constituents of the latter are missing (e.g. *Paripteris pseudogigantea*, the *Neuropteris obliqua* group, *N. heterophylla*, and *Laveineopteris rarineris*).

The assemblages from the Iberian Peninsula also have a distinctive character, usually clustering quite separately from the rest of the areas analysed. Examining the database in detail shows that they are mainly of very low diversity but, at least in the Duckmantian-Bolsovian, include some endemic taxa (*Laveineopteris guadiatensis*, *Neuropteris resobae*). A further investigation into the Namurian and lower Westphalian neuropteroids of Iberia may well produce interesting results.

In the Westphalian D the pattern breaks down at lower stratigraphical levels. Most areas form a relatively amorphous group, which includes much of the old paralic belt, together with the Intra-Sudetic Basin, NW Spain, Turkey and N. Caucasus. The chaining structure evident in this cluster in the dendrogram suggests that there is some non-homogeneity within the group of areas, but that no clear subgroups are recognizable (although, the distinctive SW UK assemblages with *Neuropteris flexuosa* and *Macroneuropteris macrophylla* are positioned at one end of the chain). This partial reduction in palaeophytogeographical provincialism appears to correlate with the withdrawal or reduction of marine influence

from most of Europe (e.g. there are no marine bands above the middle Bolsovian in the paralic belt), and thus the disappearance of the marked distinction between the paralic and intra-montane basins. The only notable exceptions to this pattern in the Westphalian D are Saar-Lorraine (it no longer clusters with the Intra-Sudetic Basin) and the highly distinctive Zwickau assemblages.

In the Barruelian to Autunian, the cluster of areas with most diverse assemblages again seems to correlate with the major coal-producing areas, in particular the Massif Central, NW Spain and the Intra-Sudetic Basin. Saar-Lorraine seems to maintain its distinctive character, while N. Caucasus has clustered quite separately because of the presence of a number of apparently endemic taxa (although it has to be recognized that the palaeobotany of this area is far from well documented).

In conclusion, the most diverse Namurian to Bolsovian assemblages occur in the coal-bearing paralic belt of northern Europe. The coherence of this group of areas breaks down in the Westphalian D, possibly as a result of the disappearance of marine influence in these areas. In the Stephanian, a second cluster of high-diversity areas appears in the intra-montane coalfields of central and southern Europe. Saar-Lorraine (together for a time with the Intra-Sudetic Basin) retains a distinct character from these high-diversity areas, as does the short-lived Zwickau Coalfield. In general, therefore, the distribution of the neuropteroid complex supports the conclusions of Gothan (1954), that there is a clear-cut distinction between the plant fossil assemblages of the paralic and intra-montane basins. It might be tempting to use the results to justify a formal palaeophytogeographical subdivision of the Europe Palaeoarea into palaeoprovinces. However, such a move would be premature before other plant fossil groups have been subjected to similar analyses.

Endemism of individual form-genera

While there is clearly significant variation in the geographical distribution of individual species, the same is not, on the whole, so for the form-genera. Particularly the commoner form-genera (*Neuraethopteris*, *Paripteris*, *Neuropteris*, *Laveineopteris*) appear to be fairly evenly distributed. The only significant exception seems to be *Sphenoneuropteris*, which, throughout its range, has only been found in intra-montane basins. *Neurocallipteris* is also mainly restricted to intra-montane basins, but this is almost certainly just a function of it being primarily a Stephanian and Autunian taxon, in which paralic basins had all but ceased to exist in Europe.

Neuropteroids from outside Europe

This study has been exclusively on records from Europe, this being where these fronds are best known. However, there are records from other areas of the world, which we will discuss briefly here.

North America. The Carboniferous of eastern and central North America belongs to the Eurameria Palaeokingdom. It is to be expected therefore that similar if not identical neuropteroids would be found here as in Europe. The problem is that, other than in the Maritime Provinces of Canada (e.g. Bell 1938, Cleal & Zedrow 1989), the Carboniferous adpressions of North America have been very little

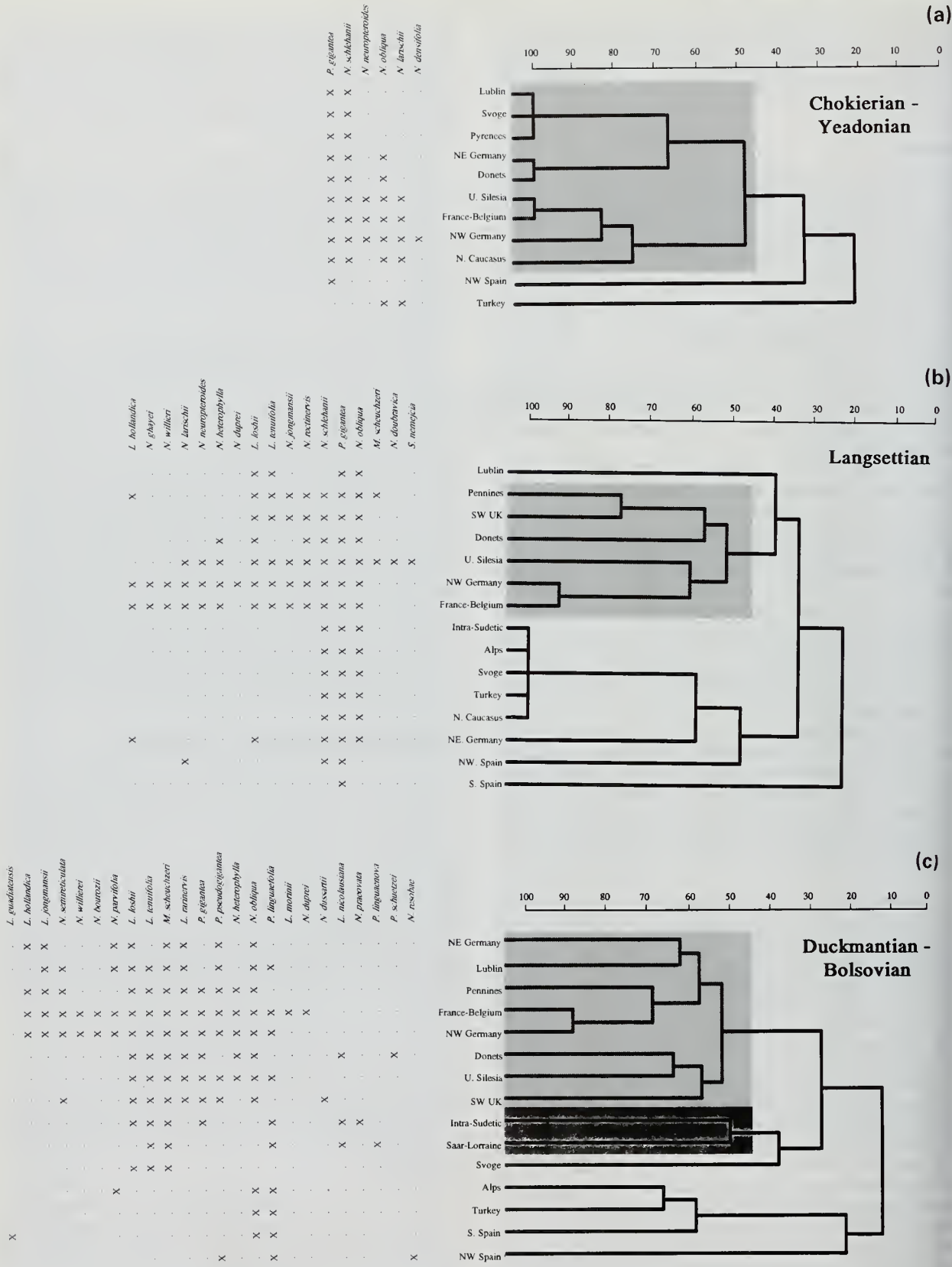


Fig. 25 Cluster analyses using geographical distributions of neuropteroid species (see text for details of methods of analysis); (a) Chokierian to Yeadonian; (b) Langsettian; (c) Duckmantian to Bolsovian.

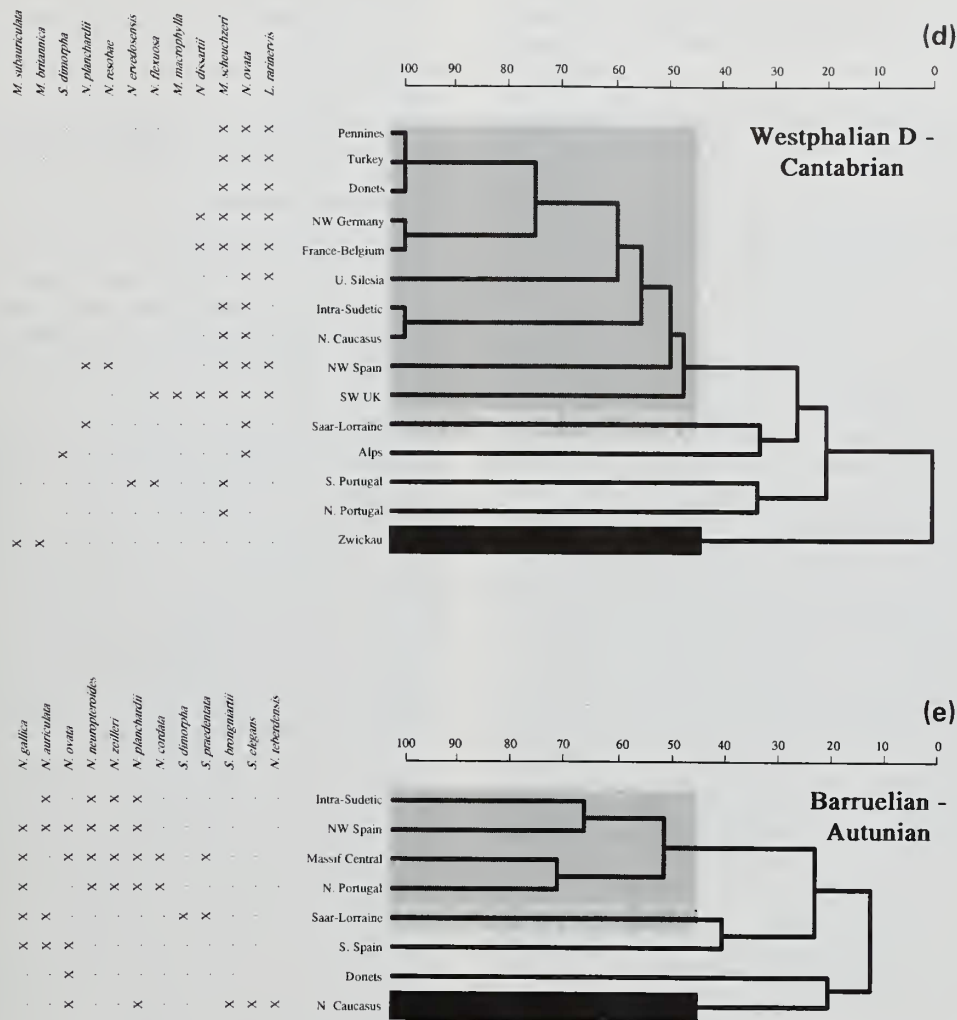


Fig. 25 cont (d) Westphalian D to Cantabrian; (e) Barruelian to Autunian.

studied, at least in recent years. There are some exceptions, such as Darrah's (1969) monograph on the Mazon Creek plant fossils, and some useful records by Gillespie *et al.* (1975), Gillespie & Pfefferkorn (1976), Gillespie & Crawford (1985) and Gillespie & Rheams (1985). These indeed suggest a close similarity to the European assemblages. However, on their own they are not really sufficient to allow a comprehensive assessment of the North American records, which is why they were not incorporated into the analysis presented in the present paper (for a further review of the North American records, see Pfefferkorn & Gillespie 1980).

The western part of North America in the Carboniferous has been assigned to two separate phytogoras, which may be referred to as the Cordillera Palaeoarea of the mid-west states and the Oregon Palaeoarea of the Pacific coastal area (Pfefferkorn & Gillespie 1980, Cleal & Thomas *in* Cleal 1991). No neuropteroids have been reported from the Oregon Palaeoarea. The Cordillera Palaeoarea is very poorly documented, with the sole exception of the plant fossils from

the Manning Canyon Shale (Tidwell 1967). Of Tidwell's records, the most significant is of *Neuropteris* cf. *pocahontas* White, which is undoubtedly a neurolethopterid similar to *N. schlehanii*. However, his record of '*Neuropteris*' *gigantea* is undoubtedly incorrect (at least one pinnule in the figured specimen has a basiscopic lobe – it may in fact be an elongate neurolethopterid) and his '*Neuropteris*' *ampelina* Tidwell is a *Eusphenopteris*.

Gondwana. There are no neuropteroids recorded from the Carboniferous of the middle and high palaeolatitudes of Gondwana (the so-called pre-*Glossopteris* and early *Glossopteris* floras – reviewed by Wagner *et al.* 1985). However, the palaeoequatorial parts of Gondwana, such as the Mérida Andes of Venezuela, the Djerada Basin of Morocco and the Sud-Oronais region of Algeria, yield typical Euramerian-type assemblages. The published records include species of *Neuropteris*, *Laveineopteris*, *Macroneuropteris*, *Paripteris* and *Neurocalipteris* (Jongmans & Deleau 1951, Jongmans 1952b,

Pfefferkorn 1977, Migier 1982). However, these are either unillustrated records, or just show small fragments, which are difficult to assess; their generic affinities are probably correct, but any further statement will have to await a more complete documentation.

Cathaysia. Although in very similar palaeolatitudes to Europe during the Carboniferous, only a few neuropteroids are found in China. The most significant from an evolutionary point of view is *Paripteris*, which seems to have first evolved in China in the late Visean (possibly Brigantian) and only later migrated west to Europe in the Namurian (Laveine *et al.* 1989, 1992). The Chinese specimens have traditionally been referred to as *Paripteris gigantea* (e.g. Li *et al.* 1974, Yang *et al.* in Wagner *et al.* 1983). However, recent work by Zhang *et al.* (1992) and Laveine *et al.* (1992) has shown that, although similar, the Chinese material is not conspecific with that from Europe and it awaits a new name.

There is also some evidence that *Neuropteris* may occur in China. There are numerous records from the Upper Carboniferous (thought to be approximately equivalent to the Stephanian in the Heerlen Classification) of North China of *Neuropteris ovata*. However, their veining is denser and the pinnules more broadly attached to the rachis than the typical Westphalian D specimens of this species from Europe, and Gothan & Sze (1933) referred them to a separate species, *N. pseudovata*. Wagner (1963) went further, to suggest that there is a close similarity between these Chinese fossils and the species which is now referred to as *Neurocallipteris neuropteroides*. This clearly raises a difficulty as to the status of the Chinese fossils, as there is no published evidence of their cuticles to prove whether they are neuropterid or neurocallipterid. In view of their relative high stratigraphical occurrence, these Chinese fossils are in clear need of revision.

Li *et al.* (1974) described some fragmentary specimens from the Namurian of China as *Lopinopteris intercalata* Sze. Laveine *et al.* (1987) have argued that they may be very closely related to *Neuropteris obliqua*. However, there will have to be a more complete documentation of the Chinese material before its taxonomic position can be confirmed.

Angara. There have been a number of records of *Neuropteris* from this palaeokindom (e.g. Neuburg 1948, Gorelova *et al.* 1973). Among the more completely known species are '*N. pulchra*' Neuburg and '*N. izylensis*' (Chirkova) Neuburg. Although only a few specimens of these species have been documented in the literature, and the illustrations of these are mostly poor, they demonstrate certain significant features of frond architecture: they have ultimate pinnae terminated by a pair of pinnules and intercalated pinnules on the penultimate rachis. These are characteristic features of the form-genus *Paripteris*, although the pinnule form and venation is rather different from any of the European or Chinese species. Also of possible paripterid affinity is '*N. dichotoma*' Neuburg, although this observation is based on the similarity of its pinnules and venation to the European species *P. gigantea*; little of its frond architecture has been documented.

Two species with very large pinnules (up to 70 mm long) have been described under the names '*N. siberiana*' Zalesky and '*N. balachonskiensis*' Gorelova. One specimen of the former, figured by Neuburg (1948: pl. 31, fig. 1), shows pinnules apparently with two basal lobes or incipient pinnules (again, the quality of the illustrations make their interpretation difficult). A comparison with *Macroneuropteris* is thus

hinted at, but far more material needs to be examined before this could be confirmed.

A rather unusual-looking species has been described as '*N. ignotus*' Gorelova in Gorelova *et al.* (1973). It has very tapered, subfalcate pinnules, spaced widely along a very wide rachis, and is quite different from anything that has been previously assigned to the neuropteroid group. A comparison with the once-pinnate peltasperm frond *Compsopteris* is possible, although without more complete material, preferably including cuticles, this affinity would be difficult to confirm.

Most of the other Angaran species that have been assigned to *Neuropteris* (e.g. '*N. tomiensis*' (Zalesky) Radchenko, '*N. orientalis*' Radchenko) are all too small and poorly illustrated to assess. As far as it is possible to make out, other than some possible paripterids, no good examples of neuropteroid fronds have been described from these floras.

Kazakhstan. The Carboniferous plant assemblages found here are intermediate in composition between those typical of Eurameria and Angara (Meyen 1987). According to both Vakhrameev *et al.* (1978) and Cleal & Thomas in Cleal (1991), about half of both species and form-genera in the Middle Carboniferous (in the Russian chronostratigraphy, equivalent approximately to the Namurian and Westphalian of the Heerlen Classification) of Kazakhstan are also found in Europe, and include some neuropteroids.

The best documented records of Carboniferous plant fossils from here are by Radchenko (1954, 1985) and Oshurkova (1967). Other than some large, isolated pinnules from the Upper Carboniferous (in the Russian sense, i.e. approximately Stephanian), identified as the Angaran species '*Neuropteris dichotoma*' Neuburg (see above), most neuropteroid-like material originates from the upper Visean and Namurian. The latter are all characterized by relatively small, vaulted, lateral pinnules with a weakly developed midvein, and a distinctive, round apical pinnule. The lateral pinnules vary to an extent in shape, from round to oval to subrectangular with a round apex, and have been assigned to various species including *Neuropteris antecessens* Radchenko non Stur, *N. heterophylla* Oshurkova non Brongniart, *N. pseudoheterophylla* Radchenko, *N. bulupalgenensis* Radchenko non Zalesky and *N. karagandensis* Borsuk. However, these morphological variants are frequently found associated together, and they almost certainly belong to one and the same species. Goganova *et al.* (1992) have recently described some remarkably complete examples of this species and found that it is fundamentally different from *Neuropteris*. They propose that the correct name is *Cardioneuropteris asiatica* (Radchenko) Goganova *et al.* Although the fronds are bipartite, producing tripinnate primary rachis branches, there are no intercalated elements between the secondary pinnules. Also, in close association were numerous *Aulacotheca*-like sporangial clusters, which in Europe are normally associated with the frond form-genus *Alethopteris*. It is clear that *Cardioneuropteris* is fundamentally different from any of the neuropteroid form-genera found in Europe.

Mention should be made of specimens recorded by Oshurkova (1967) from somewhat higher (probably Westphalian equivalent) strata under the name *Neuropteris obliqua*. Unfortunately, only one extremely small fragment was illustrated (Ibid.: pl. 15 fig. 8), which is totally inadequate for taxonomic assessment.

It seems that, other than the possible paripterid '*N.*

dichotoma and the inadequately documented *N. obliqua*, no unequivocal neuropteroid form-genera (at least in the European sense) have been recorded from Kazakhstan.

CONCLUDING REMARKS

We are minded at the end of our study to quote from the preface to John Woodward's (1729) pioneering palaeontological study; *Now, that I have been for some time engaged in Mineral Studies, with no small Application, 'tis a Pleasure to me to find that it has not been wholly without Fruit.* When we first started out on our project we intended it purely as a means of testing the robustness of the taxonomic scheme proposed by Cleal *et al.* (1990). However, we have ended up on a much longer journey into the realms of palaeogeography, biostratigraphy, palaeoclimatology and population dynamics. Trying to improve the taxonomy of a group of organisms, whether living or extinct, has its own internal logic, but we discovered that it has also provided an improved tool for understanding the pattern of the temporal and spatial distributions of the species. The distributions of the individual species were of course mostly already known, but the more general patterns were obscured by the wholly artificial generic taxonomy traditionally employed. Grouping the species into what seem to be more natural form-genera provided a context for at last seeing more clearly these more general patterns; we have been able to see the trees for the wood!

This demonstration of its geological utility of course also adds further support for the essential 'naturalness' of the revised taxonomic scheme. That a group of species responds in the same way to environmental pressures does not prove that they are closely related. However, if the species are also morphologically very similar at both the macroscopic (frond architecture) and microscopic (cuticles) levels, there must clearly be a strong likelihood that they are a genetically homogeneous group. There will always be the potential for convergent evolution to confuse the issue, especially with organs such as leaves, but by using as many morphological characters as possible it should be possible to detect this. A case in point is the close gross-morphological similarity between the mainly Westphalian D to Barruelian *Neuropteris ovata* and the mainly Stephanian C to Autunian *Neurocallipteris neuropteroides*. Some authors have gone as far as to suggest that the latter is a descendant of the former (e.g. Wagner 1963). However, their epidermal structures are very different, as are their apparent responses to environmental changes within the forests, and it is almost certain that the similarity in gross morphology merely represents convergent evolution.

Our study provides clear evidence of the long-known but often forgotten fact, that there is a close symbiotic relationship between the study of plant fossils and geology; the fossils cannot be properly understood without an understanding of the geological (sedimentological, stratigraphical, palaeogeographical) context in which they are found. Equally, the plant fossils provide invaluable palaeoecological, biostratigraphical and palaeophytogeographical data for improving our understanding of the geology. This information can then be re-cycled back to improve our understanding of the original vegetation (Cleal 1991: 223). As our study has demonstrated, this iterative process is dependent on the availability of a

robust taxonomy, not only at the rank of species but also of form-genus. Obviously, a form-genus cannot be the exact equivalent of a whole-plant genus, being based only on a single plant organ. Nevertheless, the aim should be to make a form-genus as near as possible to a phylogenetically coherent concept (Cleal 1986), and this can only be achieved by detailed morphological and taxonomic study of the fossils.

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INDEX OF GENERA AND SPECIES

This is an index of the systematic section, not the whole paper. Species which are regarded as 'good' in the sense used in this paper are shown in bold Roman type, while earlier synonyms and combinations, and species based on inadequate type specimens, are in italics. The archaic spelling variant *Nevropteris* is not distinguished in the index, and its entries are to be found under *Neuropteris*.

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